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NEW SPECIES OF CRANE-FLIES FROM SOUTH AMERICA. PART VI[1]

(Tipulidae: Diptera)

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The present paper is based almost solely upon extensive series of crane-flies taken in Brazil and Paraguay by Mr. Francisco Schade, and by Dr. John G. Myers in Venezuela and on Mount Roraima in northern Brazil. A few scattered specimens were included in materials secured by Dr. Ogloblin in Argentina and by Mr. Raymond C. Shannon in Peru. With the exception of the latter material, all of the species discussed herewith are preserved in my collection through the continued friendly interest of the entomologists mentioned.

Macromastix Osten Sacken

Macromastix (Macromastix) brasiliae sp. n.

General coloration of notum brownish yellow, the praescutum with four stripes of the ground-color that are further bordered by dark brown; mediotergite with two large brownish black areas; antennae (male) longer than body, the vestiture short and inconspicuous; wings yellowish brown, the costal border broadly darker; basal abdominal tergites yellow, the outer segments passing into black.

Male—Length, about 13 mm.; wing, 14 mm.; antenna, about 18 mm.

Frontal prolongation of head brownish yellow, lined dorsally and laterally with brown; nasus stout; palpi dark brown. Antennae (male) elongate, exceeding the body; scape enlarged, obscure yellow; pedicel small, yellow; flagellum black; flagellar segments with short, inconspicuous pale pubescence and tiny verticils that are scarcely longer than the pubescence. Head brownish yellow; vertical tubercle very large and conspicuous.

[1]Contribution from the Entomological Laboratory, Massachusetts State College.

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Mesonotal praescutum brownish yellow, with four areas of the ground-color that are conspicuously bordered by dark brown; an additional capillary black median line extends backward from the cephalic border of the sclerite for a short distance; scutal lobes brown, variegated by darker brown; scutellum dark brown; mediotergite obscure yellow, with two large, oval, brownish black areas. Vestiture of mesonotum short and inconspicuous. Pleura obscure grayish yellow, variegated by brownish clouded areas. Halteres dark brown, the base of the stem restrictedly pale. Legs with the coxae brownish gray, more or less variegated by brown; trochanters obscure yellow; femora obscure yellow; tibiae obscure yellow, the tips narrowly dark brown; tarsi black. Wings tinged with yellowish brown, the stigma, costal and prearcular regions more infuscated to provide a dark anterior border; veins brownish black, *Cu* and *2nd A* more yellowish. Venation: Sc_1 preserved; *Rs* subequal to R_{2+3}; R_3 nearly straight; cell M_1 with petiole shorter than *m*; cell *2nd A* of moderate width.

Basal abdominal tergites yellow, broadly margined laterally and more narrowly on caudal margins with blackish, the ground-color becoming more obscured and restricted on the succeeding segments, on the fifth and remaining tergites uniformly blackened; sternites more extensively yellow. Male hypopygium with the eighth sternite large and sheathlike.

Habitat: Brazil. *Holotype*, ♂, Campo Bello, Minas Geraes, September 26, 1930 (F. Schade).

Macromastix brasiliae is very different from the other Neotropical species of the genus. It is most generally similar to *M. paulseni* Philippi, differing most evidently in the short vestiture of the body and the relatively short antennae of the male sex.

Habromastix Skuse

Habromastix decolorata sp. n.

General coloration of thorax brownish yellow, the praescutal stripes slightly darker; nasus distinct; antennae (male) shorter than body; wings brownish yellow, the stigma slightly darker.

Male—Length, about 15–16 mm.; wing, 14–15 mm.; antenna, about 11–12 mm.

Female—Length, about 16 mm.; wing, 14 mm.; antenna, about 2.8 mm.

Frontal prolongation of head yellow; nasus distinct; palpi chiefly pale, the basal segment and apical portion of terminal segment, infuscated. Antennae (male) 13-segmented, only a little shorter than the body; scape and pedicel yellow; flagellum dark brown; base of first flagellar segment and incisures of succeeding three segments restrictedly pale; flagellar segments elongate-cylindrical, the basal enlargements small; besides the usual basal verticils, the segments with two other elongate setae, one before and one beyond midlength

of the segment, these verticils unilaterally arranged on the upper face; in addition to the verticils, the segments are clothed with a dense erect pale pubescence; pedicel with a group of short black setae on mesal face; terminal segment reduced. Antennae (female) shorter than thorax. Head without vertical tubercle, light brown; anterior vertex approximately twice as wide as diameter of scape at base.

Mesonotum light brownish yellow to faintly pruinose, the praescutum with scarcely indicated, slightly darker stripes; scutum somewhat more pruinose; scutellum paler testaceous brown; postnotum brownish gray. Pleura chiefly pale yellow, with a vague pruinosity. Halteres relatively long, pale, the knobs infuscated. Legs with the coxae and trochanters yellow; femora obscure yellow; tibiae and tarsi passing into brown. Wings with a strong brownish yellow tinge, cell *Sc* clearer yellow; stigma pale brown, only a trifle darker than the ground; veins yellowish brown. Venation: *Rs* relatively short and straight, a little longer than R_{2+3}; R_2 relatively long; inner ends of cells R_3 and R_5 in transverse alignment; petiole of cell M_1 shorter than *m*.

Abdominal tergites with the ground-color yellow, brightest on the basal segments, more obscure outwardly; three brownish black tergal stripes, the median one paler on basal segments, the lateral pair more distinct; sternites more bicolorous, dark-colored, their apices conspicuously obscure yellow; subterminal segments uniformly black; hypopygium yellow. Ovipositor with the valves relatively short and fleshy, the cerci broadly compressed, the hypovalvæ very small.

Habitat: Paraguay. *Holotype*, ♂, Santa Barbara, October 17, 1925 (F. Schade). *Allotopotype*, ♀. *Paratopotypes*, 2 ♂ ♂.

I am referring this fly to *Habromastix* rather than to *Tipula*, despite the presence of a distinct nasus. The only other species of the genus so far described from South America is *H. lemniscata* Alexander, readily told by the handsomely patterned wings.

Tipula Linnæus

Tipula paraguayensis sp. n.

General coloration of mesonotum opaque reddish brown, the praescutum with the median stripe polished; antennae short, 12-segmented, the basal two segments yellow, the remainder brownish black; wings with a strong brown tinge; macrotrichia of veins very scanty; cell *2nd A* narrow; male hypopygium with the basistyle produced caudad into spinous points that are setiferous to their tips.

Male—Length, 10–11 mm.; wing, 10.5–11.5 mm.

Female—Length, about 10–11 mm.; wing, about 11–12 mm.

Frontal prolongation of head of moderate length, light brown, darker outwardly; nasus distinct; palpi brownish black. Antennae 12-segmented, unusually short in both sexes, being shorter than the entire head; scape and pedicel pale yellow; flagellum brownish black; flagellar segments oval, gradually decreasing in size outwardly; terminal

segment small; verticils of basal segments less than the segments in length. Head light brown, the posterior vertex with a narrow brown median vitta; vertical tubercle entire.

Mesonotum opaque reddish brown, the median stripe polished. Pleura opaque, pollinose, almost glabrous. Halteres yellow, the knobs dark brown. Legs with the coxae pale yellow, pollinose; trochanters yellow; femora obscure yellow, the tips narrowly blackened; tibiae obscure yellow, the tips broadly brownish black; tarsi black; tibial spur formula 1–2–2. Wings with a strong brownish tinge, the prearcular and costal regions more yellowish; stigma strongly yellow, the posterior portion more brownish yellow; outer radial field narrowly infumed along margin; a narrow brown cloud on anterior cord; veins brown. Macrotrichia of veins very scanty, including a very restricted series on distal section of R_{4+5}; squama naked. Venation: *Rs* short, arcuated, shorter than R_{2+3}; vein R_3 long and nearly straight, about one-half to three-fourths longer than R_{2+3}; cell *2nd A* very narrow.

Abdomen reddish brown, in male with a conspicuous black subterminal ring; hypopygium fulvous. Male hypopygium with a U-shaped median notch, the lateral lobes obtusely rounded. Basistyle produced caudad into a slender spinous point that is densely covered with short setae to apex. A single complex dististyle; at apex strongly bent into a long pale point; near base on outer face with a flattened lobe, its apex obtusely rounded.

Habitat: Paraguay. *Holotype*, ♂, Villarica, October 14, 1925 (F. Schade). *Allotopotype*, ♀, August 16, 1924. *Paratopotypes*, 3 ♂♂, 1 ♀, September 24, 1924–October 24, 1925 (F. Schade).

Tipula paraguayensis is quite distinct from all other small species of the genus having the antennae 12-segmented. The narrow cell *2nd A* and the spinous basistyle of the male hypopygium serve to separate the fly from all other generally similar forms.

Holorusia Loew

Holorusia ringens sp. n.

Close to *lævis;* wings brownish, the costal region darker brown; a dark area at midlength of cell *M;* bases of cells *R* and *M* dark brown; male hypopygium with the tergite lacking a median lobe; outer dististyle with a small lobelike flange at near midlength.

Male—Length, about 12 mm.; wing, 13 mm.; antenna, about 3.7 mm.

Frontal prolongation of head brown; palpi dark brown. Antennae with basal flagellar segments weakly bicolorous, the apices of the segments vaguely brownish yellow; outer segments uniformly dark brown. Head brown, the posterior orbits narrowly pale, the median region of vertex narrowly blackened.

Mesonotal praescutum reddish brown, with feebly indicated darker

stripes, best indicated by narrow darker margins to the stripes and by a capillary brown median vitta; scutellum and mediotergite testaceous to brownish testaceous. Pleura brownish yellow. Halteres infuscated, the knobs more strongly so. Legs with the coxae and trochanters obscure yellow; femora brownish yellow, the tips narrowly and weakly infuscated; tibiae and tarsi darker brown. Wings brownish, the costal region darker brown; bases of cells *R* and *M*, together with a conspicuous spot at midlength of cell *M*, darker brown; stigma dark brown; narrow brown clouds at origin of *Rs* and on *m-cu;* more whitish areas in cell *M* on either side of the dark spot; a triangular pale area in outer end of cell R_3; veins dark brown. A few macrotrichia on vein R_3. Venation: Vein R_3 gently arcuated, cell R_3 being feebly constricted at midlength; distal section of vein R_{4+5} only weakly sinuous at near midlength.

Abdominal tergites reddish brown, variegated by a broken dorsomedian brown vitta; subterminal segments uniformly blackened; hypopygium yellow. Male hypopygium with the tergite lacking a median lobe, as is present in most other species of the genus. Outer dististyle long and slender, with a small, triangular, lobelike flange at near midlength. Apical beak of inner dististyle very short and blunt.

Habitat: Paraguay. *Holotype*, ♂, Villarica, December 22, 1924 (F. Schade).

This small species is allied and generally similar to *Holorusia lævis* Alexander, differing especially in the hypopygial characters, notably the structure of the tergite and outer dististyle.

Holorusia tarda sp. n.

Antennal flagellum weakly bicolorous, the apices of the basal segments obscure yellow; femoral tips not darkened; wings with a brownish tinge, the usual dark area in cell *M* nearly obsolete; male hypopygium with the outer dististyle bearing a lateral lobule beyond midlength.

Male—Length, about 12–13 mm.; wing, 13.5–14 mm.; antenna, about 5.5–5.8 mm.

Frontal prolongation of head brownish yellow; nasus distinct; palpi light brown. Antennae (male) a little less than one-half the entire body; scape and pedicel yellow; first flagellar segment brown, obscurely yellow at both ends; succeeding segments dark brown, with the apical fourth or less yellow, the amount decreasing on the outer segments; beyond the seventh segment uniformly dark brown; flagellar segments with a slight basal enlargement. Head fulvous yellow, without vertical tubercle.

Mesonotal praescutum almost uniformly fulvous yellow, without distinct stripes; interspaces with setae almost lacking, there being a few just before suture; posterior sclerites of mesonotum more buffy, with abundant short yellow setae. Pleura pale yellow, glabrous. Halteres pale, the knobs infuscated. Legs with the coxae and trochanters yellow; remainder of legs obscure yellow, the terminal tarsal segments a little darker. Wings with a brownish tinge, the prearcular and costal regions, together with stigma, slightly darker brown; a very

small, scarcely apparent dark cloud at near midlength of cell *M;* no darkened area in base of cell *R;* cells M_1 and *2nd* M_2 with an extensive, more nearly hyaline area; veins brown. Macrotrichia of veins almost lacking, except on *R*, R_1 and Sc_2+R_1. Venation: Cell R_3 only moderately constricted at near midlength; cell *1st* M_2 small, irregularly hexagonal, the two sections of M_{3+4} shortest; petiole of cell M_1 nearly twice *m*.

Abdominal tergites light brown, dark brown medially, except on basal two segments; sublateral portions of tergites narrowly dark brown; subterminal segments uniformly brownish black; hypopygium yellow. Male hypopygium with the suture between tergite and sternite obsolete on cephalic half or less. Median lobe of tergite distinct, apices of lateral lobes with conspicuous spinous setae. Outer dististyle with a lateral lobule beyond midlength. Spines of inner dististyle short and blunt.

Habitat: Paraguay. *Holotype*, ♂, Villarica, March 26, 1926 (F. Schade). *Paratopotype*, ♂, February 16, 1926.

The present fly is allied to *Holorusia lævis* Alexander, and certain related species, differing in the great reduction of the dark area in cell *M*, together with hypopygial details.

Holorusia subtarda sp. n.

Close to *tarda;* antennae shorter, the individual segments about two-thirds as long as in *tarda;* mesonotal praescutum olive brown, without evident stripes; abdominal tergites dark brown medially, more yellowish laterally; male hypopygium with the outer dististyle elongate, at about two-thirds the length slightly dilated and here provided with abundant setae.

Male—Length, about 13 mm.; wing, 15 mm.; antenna, about 4.4 mm.

Frontal prolongation of head yellow; basal segments of palpi pale brown, the terminal segment yellow. Antennae much shorter than in *tarda*, the basal flagellar segments slightly less than two-thirds as long as in that species; flagellar segments weakly bicolorous, with a little more than the basal half brown, the remainder obscure yellow; outer segments more uniformly darkened. Head brown.

Mesonotum olive brown, the praescutum without evident stripes; posterior sclerites of mesonotum a little darker brown. Pleura yellow. Halteres pale, the knobs infuscated. Legs with the coxae and trochanters pale yellow; remainder of legs obscure yellow, passing through pale brown to brown, the tips of the individual segments not darkened. Wings almost as in *tarda*, the brown spot in cell *M* similarly small and indistinct, so the wing at first sight appears almost unicolorous.

Abdominal tergites broadly dark brown medially, pale yellow laterally; basal sternites somewhat reddish brown, the subterminal segments blackened; hypopygium yellow. Compared with *tarda*, the male hypopygium shows the following differences: Median lobe of tergite larger and more conspicuous; vestiture of lateral lobes replaced by short, blackened, spinous setae. Outer dististyle elongate, at about two-thirds the length slightly dilated and here provided with abundant

long dark-colored setae, but without a distinct lateral lobe. Blackened spicules of inner dististyle much more numerous and covering a greater area.

Habitat: Paraguay. *Holotype*, ♂, Caraveni, September 3, 1925 (F. Schade).

The chief distinctions between the present fly and the very similar *Holorusia tarda* sp. n. are indicated in the above diagnosis.

Limonia Meigen

Limonia (**Neolimnobia**) **immaculipes** sp. n.

Allied to *diva;* antennal flagellum pale; femora obscure yellow, without distinct dark annuli; wings yellowish, with a reticulate dark pattern; male hypopygium with the rostral prolongation of the ventral dististyle relatively long and slender, with three short spines at near midlength; dorsal dististyle with the tip acute.

Male—Length, about 7.5 mm.; wing, 9.2 mm.

Rostrum brownish black; palpi small, obscure dark brown, the terminal segment pale. Antennae with the scape and pedicel black; flagellum obscure yellow, the outer segments somewhat darker; basal flagellar segments subglobular to short-oval, the outer segments more elongate, the verticils exceeding the segments. Head brownish black, the narrow anterior vertex and the very narrow posterior orbits yellowish gray.

Pronotum brown, medially above narrowly pale. Mesonotal praescutum almost covered by three brown stripes that are strongly suffused with blackish before the suture, the surface of these stripes with a sparse pollen; extreme lateral margin of sclerite brownish black, bordered internally by chestnut-brown; scutal lobes obscure yellow, variegated by dark brown; scutellum light brownish testaceous; mediotergite blackened on cephalic half, more yellowish brown on posterior half. Pleura yellow, with a black longitudinal stripe extending from the propleura, across the ventral anepisternum, pteropleurite and pleurotergite to the mediotergite, as described; ventral sternopleurite a little darkened. Halteres yellow, the stem tinged with greenish. Legs with the coxae yellow, variegated at near midlength with blackish; trochanters obscure yellow; femora yellow, vaguely to insensibly darkened before the tips; remainder of legs obscure yellow, the terminal tarsal segments narrowly darkened. Wings yellowish, with a muscose-reticulate pattern of brown, as in the *diva* group; veins brown, including those of the cord and radial field, not light yellow as in *diva*. Venation: Cell *1st* M_2 subequal to or shorter than the veins beyond it; vein *2nd A* gently sinuous, the cell at outer end not so pointed as in *diva*.

Abdominal tergites obscure yellow, the sternites clearer yellow. Male hypopygium with the rostral prolongation of the ventral dististyle relatively long, with three short stout spines that are closely grouped at near midlength of the prolongation. Dorsal dististyle acute at apex.

Habitat: Brazil. *Holotype*, ♂, Campo Bello, Minas Geraes, December 20, 1930 (F. Schade).

Limonia (*Neolimnobia*) *immaculipes* is closely allied to *L.* (*N.*) *diva* (Schiner) and a group of closely allied forms, as *L.* (*N.*) *muscosa* (Enderlein) and *L.* (*N.*) *tricincta* (Alexander). The almost immaculate legs of the present fly will readily separate it from the species above listed.

Limonia (**Neolimnobia**) **hypocrita** sp. n.

General coloration gray; praescutum with the stripes poorly defined, especially the lateral pair; fore femora with tips blackened, middle and hind femora with a narrow, subterminal, brownish black ring; wings with a conspicuous, loosely reticulate, brown pattern; male hypopygium with the rostral spines short and stout, the outer a little shorter.

Male—Length, about 6.5 mm.; wing, 7.8 mm.

Female—Length, about 6.5 mm.; wing, 8.5 mm.

Rostrum and palpi black. Antennae with scape and pedicel black, the flagellum brownish black; basal flagellar segments short-oval, the outer segments more elongate-oval; terminal segment about one-third longer than the penultimate. Head gray; anterior vertex at narrowest point a little narrower than the diameter of scape.

Mesonotum gray, the praescutum with stripes poorly indicated, including a median pair that become confluent before the suture; lateral stripes obsolete or nearly so; scutellum and mediotergite clearer silvery gray, the latter with a median, dark brown vitta. Pleura gray. Halteres relatively short, dark brown, the base of stem light yellow; in female, the stem more extensively pale. Legs with the coxae darkened and pruinose basally, the apices yellow; trochanters yellow; femora yellow, the tips of the fore femora narrowly blackened; middle and hind femora with a narrower and less distinct subterminal ring; remainder of legs obscure yellow, the tips of tibiae and the outer tarsal segments darkened. Wings whitish subhyaline, with a conspicuous, loosely reticulate, brown pattern, including about six or seven dashes in cell *C*, with additional transverse lines in all other cells excepting *1st* M_2; in the basal field, these areas in approximate alignment across the wing-disk; veins brown, costa more yellowish. Venation: Sc_1 ending opposite origin of *Rs;* the supernumerary crossvein in cell R_3 at or beyond midlength of cell; *m-cu* shortly before fork of *M*.

Abdomen chiefly dark brown, the caudal margins of tergites very narrowly pale. Male hypopygium with the caudal margin of tergite with a deep U-shaped notch. Rostral spines of ventral dististyle short and stout, the outer about one-fourth shorter than the inner, placed close together on basal half of prolongation. Gonapophyses with the mesal-apical lobe strongly curved. Ovipositor with the cerci short and slender; genital segment obscure yellow, the hypovalvae darkened basally.

Habitat: Brazil. *Holotype*, ♂, Campo Bello, Minas Geraes, October 27, 1930 (F. Schade). *Allotopotype*, ♀, October 12, 1930.

Limonia (*Neolimnobia*) *hypocrita* is conspicuously different from all other described members of the subgenus in the gray coloration of the head and thorax and in the pattern of the legs. Despite the reticulate wing-pattern, it appears to be somewhat closer to *L.* (*N.*) *translucida* (Alexander) than to members of the *diva* group.

Limonia (**Dicranomyia**) **mutata** sp. n.

Belongs to the *tristis* group; general coloration gray, the praescutum with a median brown stripe; halteres pale, the knobs infuscated; tibiae and tarsi black; wings whitish, without stigma; abdomen black, the hypopygium brightened; male hypopygium with the tergite transverse, the caudal margin gently emarginate; rostral prolongation unblackened, the spines arising close together.

Male—Length, about 5.5 mm.; wing, 7 mm.

Female—Length, about 6.5 mm.; wing, 7 mm.

Rostrum dark gray; palpi black. Antennae black throughout; flagellar segments oval. Head gray.

Mesonotum gray, the praescutum with a median stripe that is slightly more brownish. Pleura dark gray. Halteres pale, the knobs infuscated. Legs with the coxae and trochanters brown, the former more pruinose; femora brownish black, the bases of the middle and hind pairs somewhat paler; tibiae and tarsi black. Wings whitish, without stigma; axillary region weakly darkened; veins pale brown. Venation: Sc_1 ending opposite or just beyond origin of R*s*, Sc_2 close to its tip; cell *1st* M_2 long, subequal to or longer than vein M_{1+2} beyond it; *m-cu* shortly before fork of *M*.

Abdomen black, the hypopygium brightened. Male hypopygium with the tergite transverse, the caudal margin weakly emarginate. Basistyle with a single small lobule, additional to the ventromesal lobe. Ventral dististyle small, the rostral prolongation stout; two spines placed close together a short distance back from the tip of the prolongation; spines pale, subequal in length, without conspicuous basal tubercles. Dorsal dististyle moderately curved, the tip acute. Gonapophyses with the mesal-apical lobe blackened.

Habitat: Brazil. *Holotype*, ♂, near Mount Roraima, sweeping in the savannah along the course of the Arabopo River, altitude near 3,500 feet, November 16, 1932 (J. G. Myers). *Allotopotype*, ♀. *Paratopotypes*, 5 ♂ ♀; *Paratypes*, 1 ♀, slopes of Roraima, altitude about 6,000 feet, November 19, 1932; ♀, same slopes, altitude about 7,000 feet, November 19, 1932 (J. G. Myers); Collector's Nos. 3213, 3218, 3227, 3246, 3251.

This distinct species was one of several that were taken on and near Mount Roraima by my friend, Dr. John G. Myers. The detailed notes on the botanical components of the various stations above mentioned will presumably be published in detail by Dr. Myers and will add materially to the descriptions of novelties provided in this report. *Limonia* (*Dicranomyia*) *mutata* is very different from *L.* (*D.*) *knabi* (Alexander) of Mexico and Central America.

Helius St. Fargeau

Helius (**Helius**) **myersiellus** sp. n.

Mesonotum brown, the pleura black; antennae black, the basal five flagellar segments snowy white; femora yellowish brown, the tips snowy white, subequal in width to the similarly colored tibial bases; tibial tips narrowly white; tarsi yellowish white; wings creamy, variegated with brown washes; male hypopygium with the median region of tergite produced into a quadrate flattened plate; outer dististyle with a conspicuous lateral spine on outer margin at near two-thirds the length.

Male—Length, about 4 mm.; wing, 4.5 mm.

Rostrum black, not exceeding one-half the length of remainder of head; palpi black. Antennae with scape and pedicel dark; basal five flagellar segments snowy white, the remaining segments passing into brown; longest verticils nearly twice the segments. Head black.

Mesonotum of the type crushed, chiefly dark yellowish brown, contrasting with the black pleura. Halteres with the stems blackened, except at extreme bases; knobs broken. Legs with the coxae black; trochanters dark brown; femora yellowish brown, before tips passing into black, the tips narrowly and abruptly snowy white; tibiae, at bases, subequally snowy white, beyond which point the segment is narrowly blackened, soon paling to light brown, the outer end again narrowly dark brown, with the extreme tip equally narrowly snowy white; tarsi yellowish white. Wings with the ground-color creamy, chiefly suffused with brown, the ground-color persisting in the costal field and as extensive areas before and beyond stigma; central portion of disk, along vein *M* and the cord similarly of the ground-color; stigma oval, dark brown; slightly suffused brown areas at origin of *Rs*, on anterior cord and outer radial field; veins pale, a little darker in the clouded areas. Venation: Sc_1 ending about opposite three-fourths the length of *Rs*, Sc_2 at tip of Sc_1; *Rs* long; basal section of R_{1+5} reduced; *m-cu* shortly beyond fork of *M*.

Abdomen, including the hypopygium, black. Male hypopygium with the median region of tergite produced into a quadrate flattened plate, its margin truncate. Basistyle with a slender lobe on mesal face beyond midlength. Outer dististyle fleshy, bearing a conspicuous lateral spine on outer margin at near two-thirds the length. Inner dististyle much shorter and very slender, appearing as a simple glabrous

rod. Interbase appearing as a slender, gently curved, simple rod, the tip obtuse.

Habitat: Brazil. *Holotype*, ♂. Stretch of bush within sight of Mount Roraima, altitude about 3,000 feet; Maurukau to Arabopo, November 15, 1932 (J. G. Myers); Collector's No. 3205.

Helius (*Helius*) *myersiellus* is named in honor of the collector, Dr. John G. Myers, to whom I am greatly indebted for invaluable cooperation in my studies on the Tipulidae from many parts of the world. The present species is so distinct from all other species that it requires no comparison with any other so far made known.

Limnophila Macquart

Roraimomyia subgen. n.

Characters as in *Limnophila* s.s. but with wings and halteres totally lacking.

Type of subgenus: *Limnophila* (*Roraimomyia*) *permonstrata* sp. n.

The group is undoubtedly close to *Limnophila*, the structure of the male hypopygium being much like that of *Limnophila roraima* Alexander, likewise from Mount Roraima. The total loss of both the wings and halteres marks the extreme tendency in this direction in the Tipulidae, though approached by the genus *Alexandrella* Tonnoir (Rec. Canterbury Mus., Christchurch, 3: 27–30, Pl. 3; 1926) of New Zealand, where both wings and halteres are represented by rudiments.[2] The present fly is one of several unusually interesting Tipulidae taken by Dr. Myers on Roraima. The only other previous records from this "Lost World" mountain are contained in a paper by the writer (Amer. Mus. Novit., No. 491: 1–6, Figs. 1–18; 1931).

Limnophila (**Roraimomyia**) **permonstrata** sp. n.

Without wings or halteres; general coloration brownish gray; legs black.

Male—Length, 3 mm.

Rostrum black, pruinose; palpi black. Antennae black throughout; flagellar segments short and crowded. Head black, sparsely pruinose; anterior vertex relatively wide.

Mesonotum flattened, entirely brownish gray. Distinctions between individual sclerites of mesonotum scarcely evident. Pleura restricted in area, gray. Halteres and wings lacking. Legs with the

[2]The name *Alexandrella* Tonnoir being preoccupied, I take this opportunity to propose the new term, *Tonnoiraptera* n. n., for the group in question.

coxae elongate, black, sparsely pruinose; remainder of legs black, moderately hairy.

Abdomen dark gray. Male hypopygium with the outer dististyle slightly bifid at tip, the outer surface with long erect pale setae. Aedeagus spiraliform, inside a broad-based sheath.

Habitat: Brazil. *Holotype*, ♂, Summit of Mount Roraima, altitude about 8,500 feet, November 20, 1932 (J. G. Myers). *Paratopotypes*, 3 ♂♂; Collector's No. 3269.

"Running very actively over the ground, in the lower places, especially sandy spots near the lagoons. Not uncommon, but patchy in distribution.—*J. G. Myers.*"

Shannonomyia Alexander

Shannonomyia roraimensis sp. n.

General coloration of entire body dark brown or brownish black; antennae black throughout, flagellar segments short and crowded; front and narrow posterior orbits gray; wings with a strong brown tinge, the stigma and a vague clouding along cord somewhat darker; *Rs* and its branches unusually glabrous; *m-cu* more than one-half its length beyond fork of *M;* cerci very slender.

Female—Length, about 7.5 mm.; wing, 6 mm.

Rostrum and palpi black. Antennae black throughout; flagellar segments short and crowded, the whole antennae only about one-half longer than the head. Head dark gray, the broad front and very narrow posterior orbits silvery gray.

Prothorax and mesothorax dark brown, the surface slightly pollinose, the pleura a trifle more pruinose. Halteres dusky. Legs dark brown, relatively stout. Wings with a strong brown tinge, the stigma and a vague clouding along cord somewhat darker; veins brown. Macrotrichia of veins beyond cord unusually sparse, being lacking on *Rs* and its branches, excepting the distal section of R_5 where there are about 55 distributed the entire length of the vein; on *M* with series on distal ends of outer sections of veins M_{1+2} and M_3; a few trichia near outer end of vein *2nd A*. Venation: Sc_1 ending at near three-fourths the length of *Rs*, Sc_2 not far from its tip; R_2 subequal to R_{1+2}, immediately before the fork of R_{3+4}; *m-cu* more than one-half its length beyond the fork of *M*.

Abdomen brownish black, the ovipositor with very slender cerci that are darkened at bases, the tips horn-colored.

Habitat: Brazil. *Holotype*, ♀, Mount Roraima, summit, altitude about 8,500 feet (D. Vesey-FitzGerald); Myers' No. 3308.

Shannonomyia roraimensis is very different from the other regional species of the genus in the uniformly dark coloration of the body and appendages, the strongly suffused wings, and the glabrousness of the veins beyond the cord, which here is

more marked than in any others of the more than a score of Neotropical species of the genus. In its general appearance, the present fly resembles *S. jaffueli* Alexander, of Chile, yet is very different in the features diagnosed.

Hexatoma Latreille

Hexatoma (**Eriocera**) **roraimella** sp. n.

Allied to *kaieturensis;* femora yellow, the tips narrowly and very weakly darkened; wings pale brown, with indications of a pale, diffuse yellow band before the level of cord; macrotrichia of veins usually sparse, with none on R_3 or R_4; R_2 at fork of R_{3+4}.

Male—Length, about 17 mm.; wing, 14 mm.

Rostrum dull orange; palpi dark brown. Antennae with scape orange; pedicel dull yellow; flagellum brownish black, the proximal end of the first segment paler. Head orange; vertical tubercle entire.

Mesonotal praescutum golden-yellow, with four more brownish stripes, the intermediate pair divided by a narrow brown line; posterior sclerites of notum chiefly testaceous-yellow, the scutal lobes somewhat darker. Pleura brownish yellow, the dorsal pleurites darker. Halteres with the stem pale yellow, the knob brown. Legs with the coxae and trochanters brownish yellow; femora yellow, the tips narrowly and very weakly darkened; tibiae yellow, the tips very narrowly darkened; tarsal segments one and two yellow, the tips narrowly darker; outer segments more uniformly darkened. Wings pale brown, with indications of a pale, diffuse yellowish band before level of cord; stigma oval, brown; veins yellow. Macrotrichia of veins unusually sparse, there being none on R_{1+2}, R_3, R_4 or R_{2+3+4}; a scattered series of about eight or nine trichia on distal section of R_5. Venation: R_2 at fork of R_{3+4}; R_{1+2} about one-half R_{2+3+4}; *m-cu* just beyond fork of M.

Abdominal tergites reddish, somewhat darker brown laterally; sternites more yellowish.

Habitat: Brazil. *Holotype*, ♂, Slopes of Roraima, altitude about 5,000 feet, November 19, 1932, near small stream (savannah) edged with coarse ferns (J. G. Myers).

The nearest ally of the present fly is *Hexatoma* (*Eriocera*) *kaieturensis* (Alexander) which differs in the larger size, the differently colored femora with a distinct darkening at near midlength, and the venation, with R_2 equal in length to R_{2+3}. In both of these species, the trichia of the veins of the radial field are unusually sparse.

Hexatoma (**Eriocera**) **ogloblini** sp. n.

Body and appendages entirely deep black, with the exceptions of the light brown basal flagellar segments, and the abruptly bright yellow wing-bases.

Female—Length, about 17 mm.; wing, 13 mm.

Rostrum and palpi black. Antennae with scape and pedicel black; flagellar segments one and two, together with base of three, light brown; remaining antennal segments black; antennae (female) apparently only 7-segmented, the penultimate segment twice as long as the last and probably resulting from the fusion of two segments. Head black.

Thorax, including legs and halteres, entirely dull, deep black. Wings black, with a conspicuous, bright yellow band at base, including the entire prearcular region excepting the extreme base, as well as the very narrow bases of cell *C* and the Anal cells; this bright color is more extensive along the costal border, thence crossing the wing obliquely to the axillary region; Anal cells and centers of cells *R* and R_1 a trifle paler; veins black. Venation: Cell M_1 lacking; vein *2nd A* sinuous on outer third.

Abdomen, including ovipositor, black.

Habitat: Argentina. *Holotype*, ♀, Experiment Station, Loreto, Misiones, April 18, 1932 (A. Ogloblin). *Paratype*, ♀, with the type; in the Bruch Collection.

This striking fly is named in honor of the collector, Dr. Alejandro Ogloblin. I owe this material to the continued friendly interest of my old friend, Dr. Carlos Bruch. By my key to the Neotropical species of *Eriocera* (Psyche, 21: 34–37; 1914), the present fly runs to *nigra* (Wiedemann) of Brazil. I have seen the types of the latter species and have found the yellow color at the wing-base, indicated in the original description, is so limited as to be barely evident. In the present fly, this color is broad and very conspicuous. There is no other described *Eriocera* closer to the present species than *nigra*.

Ischnothrix Bigot

Ischnothrix brevisector sp. n.

General coloration dark brown, the mediotergite and pleura more pruinose; antennae black; wings with a strong yellowish brown tinge, the narrow stigma slightly darker brown; *Sc* short; *Rs* very short, angulated at near midlength; R_3 oblique; abdominal sternites conspicuously dimidiate, black, the incisures broadly yellow.

Female—Length, about 8 mm.; wing, 7.5 mm.

Rostrum obscure yellow; palpi black. Antennae with scape and pedicel brownish black, the flagellum black; flagellar segments elongate-cylindrical, with short setae and verticils. Head gray.

Mesonotum chiefly dark brown, very sparsely dusted with a yellowish gray pollen, the median region of praescutum still darker brown; posterior sclerites of mesonotum somewhat clearer gray. Pleura dark, heavily gray pruinose. Halteres brownish yellow, the knobs dark brown. Legs with the coxae brownish gray; trochanters brownish yellow; remainder of legs passing through brown to black on the tarsi. Wings with a strong yellowish brown tinge, the narrow stigma slightly

darker brown; veins dark brown. Venation: *Sc* short, Sc_1 ending just beyond origin of R*s*, Sc_2 lying an equal distance before this origin; *Rs* very short for a member of this group, being about one-half longer than the basal section of R_5, strongly angulated at near midlength; R_3 oblique, approximately one-half the petiole of cell R_3; veins issuing from cell *1st* M_2 long; *m-cu* at or just before midlength of cell *1st* M_2. Both wings of type show an adventitious (or possibly supernumerary) crossvein in cell *Sc* near outer end.

Abdominal tergites brownish black, the caudal margins of the segments narrowly pale; sternites conspicuously dimidiate, black and obscure yellow, the former color occupying the central portion of the segments, the latter the broad incisures. Ovipositor with the cerci blackened basally, the tips reddish horn color; hypovalvae compressed, yellow, narrowly darkened basally.

Habitat: Venezuela. *Holotype*, ♀, Silla de Caracas, altitude 1,900 meters, in cloud forest, December 21, 1930 (J. G. Myers).

The only regional species of *Ischnothrix* is *I. lloydi* (Alexander) of Colombia (Andes, Santa Marta), which is very distinct from the present fly in the venation of the radial field, notably the short subtransverse R_3 and the much shorter R_4. The generally similar Chilean species *I. ignithorax* Alexander and *I. mesocera* Alexander are very distinct in the elongate *Sc* and *Rs*.

Teucholabis Osten Sacken

Teucholabis (**Teucholabis**) **retusa** sp. n.

General coloration black, including the antennae, legs and knobs of halteres; wings narrow, faintly grayish, the oval stigma pale brown; male hypopygium with the lobe of the basistyle obtusely rounded, without spine.

Male—Length, about 3.5 mm.; wing, 3.8 x 1.1 mm.

Rostrum and palpi black. Antennae black throughout; flagellar segments oval, the verticils long and conspicuous. Head opaque dark gray.

Pronotum and anterior lateral pretergites testaceous-yellow. Mesonotum and pleura brownish black. Halteres obscure, the knobs infuscated. Legs black throughout, the segments with long erect setae. Wings much narrower than in *parishiana*, with a faint grayish tinge; stigma oval, pale brown; veins dark brown. Venation: R_2 subequal to R_{2+3+4} and R_{1+2}; last section of M_{1+2} arched where it leaves cell *1st* M_2; *m-cu* at fork of *M*.

Abdomen, including hypopygium, black. Male hypopygium with the lobe of basistyle obtusely rounded, without an acute spine, as in *parishiana*. Outer dististyle unusually long and slender.

Habitat: Peru. *Holotype*, ♂, Iquitos, March–April 1931 (R. C. Shannon).

The nearest described ally of the present fly is undoubtedly *Teucholabis* (*Teucholabis*) *parishiana* Alexander, likewise from Iquitos, which is readily told by the broader wings and different structure of the hypopygium.

Gonomyia Meigen

Gonomyia (Lipophleps) schadeana sp. n.

Belongs to the *cinerea* group; rostrum black; thoracic pleura yellow, with two brown lines; wings with stigma small but distinct; *Sc* short, Sc_1 ending before origin of *Rs* a distance greater than the length of the latter; male hypopygium with the outer dististyle provided with a blackened basal spine; dorsal style a simple spine that is about twice as long as a similar spine on the inner dististyle.

Male—Length, about 3.5 mm.; wing, 3.8 mm.

Described from an alcoholic specimen.

Rostrum and palpi black. Antennae with scape and pedicel yellow, darkened beneath; flagellum pale brown, the verticils elongate. Head yellow, the center of the vertex extensively infuscated.

Pronotum yellow, lined with brown on lateral portion. Lateral pretergites pale yellow. Mesonotum dark brown, the praescutum margined with paler brown; scutal lobes dark brown, the median area yellow with a further median brown dash; scutellum infuscated, margined caudally with yellow; mediotergite dark brown, variegated with obscure yellow at near midlength. Pleura yellow, with two narrow, dark brown, longitudinal stripes, the more ventral one broader. Halteres yellow, the knobs weakly infuscated. Legs with the coxae pale, the apex of fore coxa and base of midcoxa darkened; trochanters yellow; remainder of legs broken. Wings with a yellowish tinge, the basal portions slightly more infuscated; costal region yellowish white; stigma small, oval, darker brown; a scarcely indicated dark seam along cord; veins pale brown, more yellowish in the basal and costal portions. Venation: Sc_1 ending before origin of *Rs* a distance slightly greater than the length of the latter; *Rs* less than one-half the length of its anterior branch.

Abdominal tergites dark brown, the caudal margins of the intermediate segments paler. Male hypopygium with the outer dististyle bearing a blackened basal spine that is more than one-third the length of the paddlelike outer arm of the style, the latter further provided with a single small spine in the axil. Inner style a hemispherical fleshy mass, prolonged caudally into a strong, thornlike spine that is about one-half longer than the basal spine of the outer dististyle. Dorsal style a slender, simple spine, curved at base, about twice the length of the thorn of the inner dististyle.

Habitat: Paraguay. *Holotype*, alcoholic ♂, Villarica, 1931 (F. Schade, through Dr. G. C. Crampton).

I take great pleasure in naming this fly in honor of my friend, Mr. Francisco Schade. The species is allied to *Gonomyia* (*Lipophleps*) *æquispinosa* Alexander (Paraguay), differing in the darker wing-stigma, shorter *Sc* and in the details of the male hypopygium. In *æquispinosa*, the spines of the dorsal dististyle and the inner style are both small and subequal in size, while the outer dististyle is a simple, elongate, unarmed blade.

Trentepohlia Bigot

Trentepohlia (**Paramongoma**) **roraimicola** sp. n.

General coloration of thorax light brown; antennae black throughout; legs brown, the tarsi slightly paler; wings with a dusky tinge, restrictedly patterned with darker brown, including the stigma and a seam at origin of *Rs*; vein R_3 unusually erect, so cell R_2 is longer than wide at costa; cell *1st* M_2 elongate, the basal section of M_3 long and arcuated.

Male—Length, about 6.5 mm.; wing, 7.5 mm.

Rostrum dark brown; palpi black. Antennae black throughout; flagellar segments oval to subcylindrical, with inconspicuous verticils. Head dark brown, sparsely pruinose; anterior vertex narrow.

Mesonotum and pleura almost uniformly light brown, the dorsopleural region a little darker. Halteres dirty white. Legs with the coxae light brown; trochanters testaceous; remainder of legs brown, the tarsi slightly paler. Wings with a dusky tinge, the stigma and a seam at origin of *Rs* darker brown; narrower and less evident clouds along cord and on vein *m;* veins brown. Macrotrichia of veins very sparse, beyond cord with a restricted series on vein $R_{1+5} + M_{1+2}$ and on the distal section of R_{1+5}. Venation: Sc_1 ending shortly before R_2, the latter at fork of R_{3+4}; R_3 unusually erect, longer than the distance on costa between veins R_{1+2} and R_3; vein R_4 long-extended; cell *1st* M_2 elongate, the upper face (vein $R_{1+5} + M_{1+2}$) longer than R_{2+3+4}; basal section of M_3 elongate, arcuated, about one-third longer than *m-cu*.

Abdominal tergites brown, the sternites obscure yellow, the outer sternites with the caudal borders weakly darkened.

Habitat: Brazil. *Holotype*, ♂, Mount Roraima, summit, altitude about 8,500 feet (D. Vesey-FitzGerald); Myers' No. 3307.

Trentepohlia (*Paramongoma*) *roraimicola* is abundantly distinct from all other species in Tropical America, the most conspicuous features being the combination of unvariegated legs, slightly patterned wings, and the venation, especially the erect vein R_3 and the elongate cell *1st* M_2.

Cryptolabis Osten Sacken

Cryptolabis (**Cryptolabis**) **schadei** sp. n.

Mesonotum brown, the praescutum lined with blackish, including median and sublateral stripes of this color; antennal flagellum chiefly obscure yellow; halteres pale yellow; legs yellow, the tips of the femora and tibiae, and all of tarsi excepting proximal ends of basitarsi, dark brown; wings tinged with grayish yellow, the linear stigmal seam and an axillary area brown; macrotrichia of cells abundant; *Rs* elongate, in alignment with R_5; R_2 longer than R_{2+3}.

Female—Length, about 4 mm.; wing, 5 mm.

Rostrum and palpi brown. Antennae with scape and pedicel dark brown, the flagellum obscure yellow; flagellar segments subcylindrical to somewhat oval, with long conspicuous verticils that exceed the segments in length. Head pale brownish testaceous.

Pronotum and lateral pretergites yellowish white. Mesonotum brown, the praescutum with a narrow blackish median line and less distinct sublateral stripes of the same color, the latter crossing the suture onto the lateral margins of the scutal lobes; centers of scutal lobes brown; posterior sclerites of mesonotum infuscated. Pleura chiefly blackened, the dorsopleural region testaceous, the ventral sternopleurites paling to light testaceous brown. Halteres pale yellow. Legs with the coxae brownish testaceous; trochanters yellow; femora yellow, the tips narrowly dark brown; tibiae obscure yellow, the tips narrowly darkened; tarsi dark brown, the proximal end of basitarsus yellow. Wings tinged with grayish yellow, the prearcular and costal regions clearer yellow; an elongate stigmal seam and an axillary area brown; veins brownish yellow. Macrotrichia of cells numerous, especially beyond the cord and in outer ends of cells *Cu*, *1st A* and *2nd A*. Venation: *Rs* elongate, sinuous on distal half; R_2 oblique, a little longer than R_{2+3}; *Rs* in direct alignment with R_5; cell M_2 deep, its petiole shorter than *m-cu*.

Abdomen brown, the ovipositor paler.

Habitat: Brazil. *Holotype*, ♀, Campo Bello, Minas Geraes, October 5, 1930 (F. Schade).

Cryptolabis (*Cryptolabis*) *schadei* is named in honor of the collector. It is most nearly allied to species such as *C.* (*C.*) *chilota* Alexander and *C.* (*C.*) *spatulata* Alexander in the elongate *Rs* in perfect alignment with vein R_5, differing from all described species in the pattern of the thorax, legs and wings.

Toxorhina Loew

Toxorhina (**Toxorhina**) **mendosa** sp. n.

General coloration buffy brown, the praescutum with three, narrow, dark brown stripes; halteres pale yellow; legs yellow, the tips of the tibiae conspicuously blackened; male hypopygium with the basistyle

produced at apex on mesal face into a flattened, dark-colored lobe; arms of aedeagus short, obtuse.

Male—Length, excluding rostrum, about 7 mm.; wing, 5.5 mm; rostrum, 4.2 mm.

Rostrum elongate, dark brown. Antennae black throughout. Head brownish gray.

Pronotum black. Mesonotal praescutum buffy brown, with three, narrow, dark brown stripes; scutal lobes conspicuously marked with brown; posterior sclerites of mesonotum more pruinose. Pleura brown, the dorsal sclerites darker, the ventral sternopleurite a little darker than the dorsal portion. Halteres pale yellow. Legs with the coxae dusky basally, more yellowish at tips; trochanters yellow; femora obscure yellow; tibiae obscure yellow, the tips conspicuously blackened; tarsi pale brown, the outer segments blackened. Wings subhyaline; axillary region weakly darkened; veins dark brown, the prearcular region and veins *Sc* and *R* more yellowish. Venation: Sc_1 ending opposite origin of *Rs*; *m-cu* before fork of *M*.

Abdomen brownish yellow, the caudal and sublateral portions of the segments restrictedly darkened; outer segments, including hypopygium, more uniformly darkened. Male hypopygium with the apex of basistyle on mesal face produced into a flattened, dark-colored lobe, much as in *fragilis*. Dististyle much as in *fragilis*, the base terminating in two blunt blackened spinulose points, the rostral blade flattened and bearing a conspicuous toothed flange near base. Aedeagus with the arms short, obtuse.

Habitat: Brazil. *Holotype*, ♂, Campo Bello, Minas Geraes, January 16, 1931 (F. Schade).

Toxorhina (*Toxorhina*) *mendosa* is most nearly allied to *T.* (*T.*) *fragilis* Loew (Greater Antilles) in the general coloration and blackened tips of the tibiae, differing in the structure of the male hypopygium, especially the details of the dististyle and the obtuse arms of the aedeagus, in *fragilis* these being longer, lyriform, with each arm drawn out into an acute point.

THE SEVENTH AMERICAN SCIENTIFIC CONGRESS

A belated notice (July 12, 1935) has been received of the Seventh American Scientific Congress to be held in Mexico City from the 8th to the 17th of September of this year. This is an International effort to bring North and South American scientists together. In this country it is sponsored by the Secretary of State and the American Association for the Advancement of Science. Dr. A. C. Baker has been appointed official delegate from the Association of Economic Entomologists. Mr. Charles C. Plummer has been appointed official delegate from this Society. Both are stationed at the Bureau's Laboratorio Entomologico, Colonia Anahuac, Mexico, D. F.—THE MANAGING EDITOR.

THE MYOGENIC AUTOMATISM OF THE CONTRACTION OF THE HEART OF INSECTS

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It was observed by Carlson (1904) that when the median, cardiac nerve cord (ganglionic) of the "horseshoe crab," *Limulus* is isolated up to the third segment the amplitude of the contractions of the anterior segments is about halved. He also noted, in a now classical but simple series of experiments (1905) that lesion of the median nerve cord and the two lateral nerves in any segment of the heart destroyed the coordination of the two ends of the heart on either side of the lesion; and conversely, a cross-section of the heart in any segment, leaving the longitudinal nerves intact, did not interfere with the coordination. "The abolition of coordination by sectioning the longitudinal nerves is immediate and permanent. Both ends of the heart continue to beat but with independent rhythm. Therefore, conduction of the heart in this animal is in the nervous and not in the muscular tissue." This work was repeated on the isopod, *Ligia oceania*, by Alexandrowicz (1932a) with the same results. Carlson further found that total extirpation of the median nerve and the lateral nerves caused the heart to cease beating immediately. It was concluded that the heart beat as well as the transmission of that beat throughout the heart is of purely nervous origin and the result of rhythmic nervous impulses sent out from the median cardiac nerve which contains neural cell bodies. Carlson and Meek (1908) later found that the embryonic heart of *Limulus* begins to beat before any anlage of the dorsal median cardiac nerve cord, the dorsal nerve plexus, or of the lateral cardiac nerves appears. They then concluded that there takes place a transfer of automatism from the myocardium to the nervous tissue at some stage. This observation is sufficient to show that myocardial transmission is at least feasible.

Hoshino (1925), disputed the results of Carlson. By employing Carlson's method in the preparation of the *Limulus* heart for exposure, his results were identical with Carlson's. But by opening the carapace 0.5 to 1.0 cm. from the dorsal median line he found that the *Limulus* heart would beat rhythmically even after the removal of the nervous bundles.

He attributed Carlson's results to the damaging of the heart by the tearing of the suspensory ligaments attaching it to the carapace.

Garrey (1933) found that stimulating one of the lateral nerves of the heart of *Limulus* by mild faradic shocks, "the neurogenic beats of the homonomous half of the heart were superposed on a raised tetanic base . . . , while those of the contralateral half were altered to a far less extent" though the rhythmic actions persisted. This was held to show that the stimulated nerve does not innervate all of the contractile elements on the same side as it would if muscular conduction were effective.

The segmented heart of *Peripatus* and the myriapods has a median cardiac nerve running on the dorsal side of the heart, similar to that in *Limulus* (Carlson, 1905). Also according to Alexandrowicz (1932b and 1934) decapod and stomatopod Crustacea possess a median cardiac nerve trunk on the dorsal surface of the heart in which ganglion cells are present. Concerning the innervation of the insect heart there are only two detailed studies at hand: that of Zawarzin (1911) on the larva of the dragonfly, *Aeschna;* and that of Alexandrowicz (1926) on the cockroach, *Periplaneta*. There are two lateral cardiac nerves and no median dorsal nerve in the above insects. Zawarzin, while describing "varicosities" in the lateral nerves of *Aeschna*, definitely asserted the absence of ganglion cells in such. Alexandrowicz, however, has photographed perikaryons with deeply staining nuclei in the lateral nerves of the cockroach.

The purpose of the present work is that of discovering whether the rhythmic heart beat of an insect is independent of possible rhythmic impulses despatched from ganglionic cells.

MATERIAL AND TECHNIQUE

Large-sized larvae of the dragonfly, *Anax junius* Drury, and in certain cases, adults of the water-bug, *Belostoma flumineum* Say, were used. A cut was made in the body cuticle, with a fine scissors, all around the circumference of the ventral part of the abdomen, and the whole ventral cuticle was then removed. The insect was placed on its back in a Ringer's solution and the tracheae and intestinal tract were carefully dissected away, thus allowing a full view of the heart. Care was taken to keep the heart adhering to the cuticle by its alary muscles and suspensory ligaments. The composition of the Ringer's solution used was: NaCl, 9 gms.; KCl, 0.2 gms.; $CaCl_2$, 0.2 gms., and distilled water, 1,000 cc.

For the experiments a 3 per cent solution of procaine HCl (Jensen &

Salsbery) in the Ringer's solution was used. In all cases, prior to the introduction of the heart preparation into the drug solutions, the heart's activity was tested in plain Ringer's, since sometimes in removing the viscera the heart wall was damaged and the pulsation would consequently be abnormal or fail. A needle syringe was used when injections into the haemolymph were made.

Intravitam staining with 0.3 per cent MB in the Ringer's was accomplished by immersing the heart, exposed as stated above and still adhering to the dorsal wall of the abdomen, for four or five hours. The stain was fixed in a saturated solution of ammonium molybdate (about 12 hours), and then washed in distilled water for a few hours.

The test for indophenol oxydase by the use of the "Nadi" reagent was best accomplished thus: the heart preparation was placed in a watch glass containing equal volumes of 0.3 per cent α-naphthol and freshly prepared 5 per cent dimethyl-p-phenylenediamine-HCl in Ringer's solution. There was just enough to cover the heart. After five minutes in such the preparation was immersed in 0.3 per cent aqueous Na_2CO_3, exposed to the air for several seconds and returned to the same solution. It was often necessary to repeat the process several times.

RESULTS

The writer supposed that the "varicosities" described by Zawarzin in the lateral cardiac nerves of *Aeschna* might be ganglion cells similar to those described by Alexandrowicz in the cockroach. An examination of the lateral cardiac nerves of *Anax* (Fig. 1) revealed neither "varicosities" nor ganglion cells, but rather a few neurilemma nuclei, *n*, sparsely scattered along the lateral nerves which, as the photograph indicates, are but large axons.

The heart of a dragonfly larva is composed of eight chambers of which the two most posterior are the largest and most powerful, possessing functional ostia and taking the blood from the haemocoele. The remaining six chambers have no functional ostia, lack alary muscles, a pericardial diaphragm, and functional ostia, but possess valves (Zawarzin). Tillyard (1917) termed the two posterior chambers the "receptive heart" and the remaining six chambers the "ventricular heart." The heart wall is musculated throughout. The chamber valves open with the systole of the more posterior chamber (i. e., anteceding) and close with lightning rapidity. The ostia close during systole and open during diastole. In all cases the pulsations were forward with no reversals. This was also true of *Belostoma*. Gerould (1933) could find no heart beat reversal in adult dragonflies.

EXPERIMENT 1. The dorsal wall of the abdomen to which the heart was adhering by its suspensory ligaments throughout its length and by its alary ligaments and alary muscles in its swollen, posterior, receptor portion, was isolated from the rest of the body and placed in the Ringer's solution. Besides acting as a control for the drug experiments, this was intended to show whether the heart would contract rhythmically with the total absence of connections with ganglionic cells. Of course, the lateral nerves were adhering but these had been found to contain no ganglion cells.

The larva was 3.5 mm. long; and the temperature 79° F. The preparation was immersed in Ringer's at 9:37 a. m. The receptive part beat fairly regularly at 60 times per minute. The pulsations ceased at 9:40 a. m., but beat regularly and rhythmically for several seconds up to a minute when the receptive part was stimulated with the point of a pin. At 9:43 a. m. the heart began to beat spontaneously and vigorously. At 9:55 a. m. the beats at the receptive part were 100 per minute. At 10:40 a. m. the receptive part pulsated at 94 per minute. At 11:11 a. m. there were 28 beats per minute at the receptive end. The beats were still vigorous and fairly regular. Then a decline in the rate began. By 11:45 a. m. the heart ceased to beat even upon stimulation. The receptive part of the heart beat generally more rapidly and with

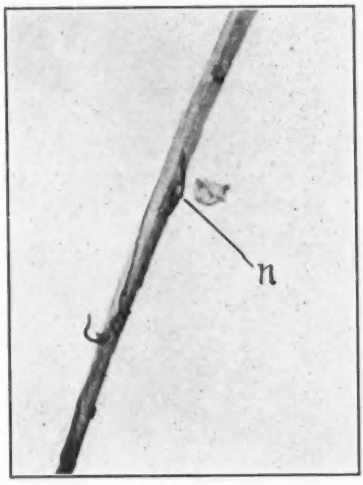

FIG. 1. Microphotograph of a part of one of the lateral nerves (isolated) innervating the heart of *Anax*. 125X. Wratten M-plate, Wratten green filter; n= a neurilemma nucleus.

less regularity than the ventricular portion. The cessation of heart beat upon first introduction into the Ringer's must have been owing to inadaptability to the foreign medium. This experiment is to be construed as evidence favoring the myogenic nature of the heart beat in these insects.

EXPERIMENT 2. A similar heart preparation as in Experiment 1. The larva (4.2 mm. long) was introduced into Ringer's solution at 10:53 a. m. The temperature was 79° F. There were 27 vigorous pulsations per minute. The beats then slowed down and ceased for a few seconds before recommencing spontaneously. The preparation was placed in one per cent procaine HCl in Ringer's at 10:55 a. m. At 10:56 a. m. there were 78 beats of the receptive part per minute. The beats were regular and continuous. At 11:45 a. m. the heart beat at

32 per minute, but only upon stimulation of the receptive end with the point of a pin. At 11:55 a. m. the ventricular part was so stimulated, and the pulsations traveled in both directions from the point of stimulation until the backward pulsation was annihilated by the stronger aroused forward pulsation from the receptive end. Spontaneous pulsations began to occur now and then. At 1:20 p. m. the heart was beating rhythmically and spontaneously at 27 per minute. A part of the ventricular heart was in a permanent systole. At 2:45 p. m. the heart was still pulsating at the same rate and fairly regularly. Stimulation of the first, second, or third chambers increased the rate. The preparation was then discarded. This preparation behaved more vigorously than the control and the experiment offers further support for the myogenic origin of the heart beat in this insect, since all ganglionic cells had been removed and procaine was added.

EXPERIMENT 3. A repetition of the preceding one, yielding similar results.

EXPERIMENT 4. A repetition of the preceding two, but using a similar preparation of *Belostoma flumineum* instead. The heart beat for four hours in a solution of one per cent procaine in the Ringer's. The preparation was discarded while the pulsation was still vigorous.

EXPERIMENT 5. The heart preparation of a 3.4 mm. *Anax* larva was introduced into a 0.0001 per cent solution of cocaine in Ringer's after having been tested in plain Ringer's. In half an hour the heart ceased pulsating in a state of systole and all capacity for stimulation was annihilated. This experiment was repeated three times with similar results. In view of the preceding experiments one should consider cocaine as definitely toxic to muscular as well as to nervous tissue.

EXPERIMENT 6. Into the lateral part of the abdomen of *Anax* were injected 0.025 cc. of ether. The heart stopped pulsating instantaneously though the limbs continued to move for several seconds after. The same result was obtained by using chloroform. The same remark that was made with reference to cocaine applies to ether and chloroform. Alvarez (1929) presents the facts that the muscle wall of the intestine ceases to contract in a saturated solution of ether and of chloroform as pharmacological "proof" for the myogenic nature of the contraction of the gut muscles. Pharmacological "proof" is very precarious in such cases, and certainly in that of saturated solutions of ether and of chloroform. The evidence offered by procaine should not be relied upon without the total removal of the ganglion cells which supplies conclusive evidence upon which pharmacological "proofs" may be tested.

EXPERIMENT 7. In view of the forward pulsation of the heart and of the myogenic nature of its beat, a possible metabolic gradient might exist along the length of the heart. The indophenol oxydase test by means of the "Nadi" reagent was carried out. Care should be taken to keep all levels of the heart at the same distance beneath the surface of the solution and to expose the whole heart equally to the air when this is desired. With these precautions taken no gradient could be observed in the heart since the whole organ stained an intense blue

making a detection of differences in color impossible. This was repeated a few times with the same results.

EXPERIMENT 8. While the heart was beating normally in the Ringer's, the alary muscles joining the heart to the cuticle were detached from the cuticle. The result was a general fair collapse of the heart wall, but the beats remained regular and rhythmic. This indicates that the heart can pulsate without alary muscle attachments. When the heart is carefully and completely removed from the body wall it generally instantly ceases to beat, though there may be a few quivers when it is in this state of collapse. This condition is irrevocable even upon artificial stimulation with a pin. The writer obtained the same results with *Belostoma*. The fine suspensory ligaments attaching the heart are thus necessary for the functioning of the heart muscle. There thus seems to be some basis for Hoshino's criticism of Carlson's results. But Carlson floored the question from such different angles (see introduction) as to make his own conclusions the more probable. Besides, Cosmovici (1925) and Rijlant (1932) were able to isolate hearts of the crayfish, of crabs, and of a lobster with no cessation of pulsation or rhythmicity.

CONCLUSIONS

The results from operation and from procaine show that the heart beat and rhythm of *Anax junius*, and probably that of *Belostoma flumineum* are independent of possible rhythmic impulses despatched from ganglionic cells.

The fine, dorsal, suspensory ligaments of the heart must be left intact on the body cuticle if the heart muscle is to function.

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ANATOMY OF CNEMIDOCOPTES MUTANS (R. AND L.), THE SCALY-LEG MITE OF POULTRY

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The scaly-leg mite of poultry has been studied under various names. The principal ones are: *Sarcoptes mutans* by Robin and Lanquetin (1859); *Sarcoptes anacanthes* by Delafond and Bourguignon (1862); *Sarcoptes changeant* by Reynal and Lanquetin (1863); *Knemidocoptes viviparous* by Fürstenburg (1870); *Dermatoryctes mutans* by Ehlers (1873); *Cnemidocoptes mutans* by Canestrini (1894).

Most of the literature on *Cnemidocoptes mutans* deals briefly with the external morphology and dwells more upon diagnosis and therapeutics. A few papers, however, notably those by Robin (1860), Fürstenburg (1870), Ehlers (1873), Norner (1882), and Haiduk (1909), deal at some length with morphology. Haiduk (1909) reviews the principal literature dealing with the species. Norner (1882) touches very briefly upon the internal anatomy. In no case, as far as known, have serial sections of any member of the genus been made. Stekhoven (1921), in a study of the biology of *Notoedres notoedres* of the rat, included several figures indicating that he had made serial sections. His material, however, must have been rather poor. The works of Vitzthum (1931) and of Sig Thor (1904 and 1931) are the most comprehensive on the anatomy of mites. Each of these papers give extensive bibliographies. In addition

to the above mentioned papers, a study of the literature dealing with the anatomy of specific forms has been of assistance. Among such works are those of Michael (1883, 1895, a and b, 1896, and 1901), Henking (1882), Nalepa (1884 and 1885), and Buxton (1921).

It was decided that a more complete study of the external morphology of *C. mutans* was desirable as a starting point for the study of the internal anatomy.

SOURCES OF MATERIAL

Cnemidocoptes mutans is present in many small poultry flocks, but is quite rare in larger establishments. The material studied was uniform and was obtained from three flocks of Rhode Island Reds, one of which had served as the source of infection for the other flocks. In *C. mutans* the females are larger and appear to greatly predominate. A total of 1,631 mites were dissected from the leg of one hen. Of these, 1,500 proved to be adult females, 39 were larvae, 27 first-stage nymphs, 48 second-stage nymphs, 2 third-stage nymphs and only 15 were adult males. The percentage of females was ninety-two but this may be rather low, since in dissection the larger and softer females are more easily destroyed. In the above figures only perfect specimens were counted. On account of the size, abundance, and lack of heavy chitinization only the females were used for this study.

TECHNIQUE

Fixatives: The fixative which seemed to be best suited for *C. mutans* was hot alcoholic Bouin's. Cold Bouin's, either aqueous or alcoholic, proved unsatisfactory. Carnoy's fluid caused too much shrinkage. Flemming's and Zenker's fluid as well as Zenker's formol were not satisfactory. The cupric-paranitrophenol fixing fluid of Petrunkevitch (1933) when used hot seemed to penetrate well.

After the removal of the picric acid in 70 percent alcohol the specimens were placed in diaphanol for two to four days. This was necessary in most cases to obtain perfect serial sections. Diaphanol tends not only to soften the chitin but if left too long may affect the tissues. The diaphanol was removed by several changes of alcohol and the specimens dehydrated to 95 percent alcohol where they were stained with eosin before completing dehydration in absolute alcohol. Mites in fresh absolute alcohol in small corked vials were placed in an incubator at 59° C. Cedar oil was poured to the bottom of the vials. After the specimens had sunk into the oil, the oil and alcohol were pipetted off and fresh warm oil added. After several hours in cedar oil the mites were placed in cedar oil and paraffin before being passed

through two or three changes of paraffin with a melting point of 56° C. A long time, one to three days, in the different solutions was found preferable to a shorter time. Under a binocular microscope, to permit orientation, specimens were embedded in paraffin in a small watch crystal (McClung, 1929). A single specimen was sectioned at a time and the sections transferred to a slide. Sections were cut at four and five microns. The eosin stain served to locate the specimens in embedding and in the paraffin ribbon. The best stain for sections was iron-haematoxylin; the best mounting medium proved to be thin damar dissolved in xylol.

A gum arabic medium (Buxton, 1921) was most satisfactory for the study of the external anatomy of fresh material. The cocain hydrochlor was not used, as I was unable to obtain it. Glycerine jelly was not a satisfactory medium except for specimens which had been treated with sodium or potassium hydroxide. Much time was consumed in carrying the mites up through the different concentrations of glycerine but the specimens were usually quite shrunken. Euparal proved satisfactory only in fixed specimens which had been dehydrated and treated with cedar oil. Fixed specimens, stained in warmed hydrochloric carmine, dehydrated, cleared in cedar oil and mounted in gum damar dissolved in xylol proved best for study of internal structures. Treatment with a cold five percent solution of sodium hydroxide destroyed the muscles and viscera and made the study of chitinous parts easier.

EXTERNAL ANATOMY

The body is colorless or light cream colored. It is convex above and below. In females filled with young near the genital operculum (Figure 2, Plate I), the convexity below is greater than the convexity above. The points of greatest convexity are just back of the tocostome on the ventral surface and farther posterior on the dorsal surface. At a point seventy-three percent of the distance from the cephalic to the caudal end of the mite a lateral indentation is present on either side in most adult specimens. It is less pronounced in larvae and nymphs. In potassium hydroxide treated specimens of *S. scabiei* from the ferret they are in approximately the same position. No transverse line on the ventral surface behind the tocostome separating the notothorax from the notogaster is present in *C. mutans*. Some specimens of *S. scabiei* of the ferret show on either side a lateral indentation and a condensation of annulations on the ventral surface posterior to the genital operculum. This may be the line which Buxton (1921) described for *S. scabiei* var. *equi*.

The length varies from 0.309 to 0.397 mm. (average 0.344 mm. for twenty-five living individuals taken from one host); the width varies from 0.250 mm. to 0.347 mm. (average 0.296 mm. of the same individuals). This variation in length is 88 microns and in width 97 microns. This variation in size corresponds closely to the variation noted by Buxton for *S. scabiei* var. *equi* (variation of 75 microns for length and 45 microns for width, based on only ten individuals). The greater range in variation in *C. mutans* may be accounted for by the

less rigidity of the body. The ratio of the length to breadth varies from 97/100 (only a single specimen of the twenty-five was shorter than broad) to 100/77.5.

Specimens fixed in hot alcoholic Bouin's generally appear slightly larger than living individuals. Two groups were fixed and measurements made of twenty-five of each are as follows:

I. Length: 0.361 mm. to 0.426 mm. (average 0.393 mm.)
Width: 0.287 mm. to 0.382 mm. (average 0.344 mm.)
II. Length: 0.346 mm. to 0.434 mm. (average 0.391 mm.)
Width: 0.281 mm. to 0.368 mm. (average 0.321 mm.)

Variation in ratio of length to breadth is 100/89 to 100/70.

Another group of twenty-five fixed in cupric-paranitrophenol have an average length of 0.387 mm. and an average width of 0.327 mm. The variation of ratio of length to width is 100/89 to 100/77.

It will be seen from these measurements that proper fixation has little effect on the actual size of the individuals—if anything, they appear slightly larger after fixation. A comparison of living and fixed specimens shows that the ratio of length to width has not been altered by fixation. In all these measurements the same method was followed. Each specimen was measured by an accurately calibrated microscope. Haiduk (1909) gave the following measurements: Length varies between 0.354 and 0.471 mm.; the breadth between 0.33 and 0.39 mm.

DORSAL SURFACE

One of the most prominent features on the dorsal surface is a pair of heavily chitinized bars (Fig. 1, Plate 1). The bars measure 0.09 mm. in length (average for ten individuals). They arise at the angle made by the pedipalpi and the base of the first pair of legs, and project posteriorly parallel to one another. At the caudal end of each bar there is a curved transverse bar forming with the longitudinal bars an inverted T (Figure I, Plate 1). The inner part of one cross bar joins its mate on the midlongitudinal axis. The heavy chitinization is less complete where the two join. In the angles of the T and also covering as much as the posterior half of the space between the horizontal bars, are punctate areas, the "Rückenschuld" of various authors, the "plastron" of others. Haiduk (1909) states that under strong magnification fine canals which break through the dorsal plate are connected with these puncturings. The impression of a canal system is seen where the caudal part of the punctate areas comes in contact with the transverse bar. A study of sections indicates that the sculpturing is superficial. In mites such areas have been thought to have a respiratory function.

Numerous ridges (Figure 1, Plate I) run in various directions on different parts of the body and some of them form scalelike structures. These scales and grooves are not necessarily identical on the two sides. They are lacking over the punctate area and for the most part between the two longitudinal bars. They are very indistinct over the anterior third of the body.

The anal opening is a terminal and slightly dorsal slit with heavy chitinous walls.

The copulatory opening is within a rounded chitinized structure about six microns in diameter and closely resembles the base of a seta. It is larger than any except the second anals, A_2. The pore is located immediately to the right, in some cases to the left, of the anterior edge of the anal slit. Specimens have been found in which the opening appears to be within the border of the anal lip. As far as known, no figures of *C. mutans* show the copulatory opening. Various authors as Gudden, Trouessart, Megnin, Haiduk, Buxton, Stekhoven, and others call attention to this copulatory opening in various mites. Hirst (1922) figured this opening in *Notoedres muris* (Syn. *N. notoedres*), but failed to include it in the drawing of the dorsal surface of *C. mutans*.

Setae: When they appear comparable in position, the setae of the various parts of the body are named following the terminology used by Buxton (1921) for *S. scabiei* var. *equi*. The setae of the capitulum and of the legs are discussed in the study of these parts. Nine pairs of setae are present on the dorsal surface. The anterior two pairs, D_2 and D_2-a, are located close together, a short distance lateral to the tips of the transverse bars (Figure 1, Plate I). At each side of the anus are located two pairs of anal setae (A_1 and A_2, Figures 1 and 2, Plate I). The second anals (A_2) are the longest (length 0.09 mm., average of twenty-five specimens) and most prominent of all the setae. Setae D_5 are located just cephalad of A_1 and A_2, forming the apices of triangles of which the anals form the bases. Setae D_4 and D_3 are cephalad and laterad to D_5. Seta D_4 is mesad to the fourth pair of legs as these show through cleared mites. The setae, L_2, are located on the dorsal surface midway between the third and fourth epimeres as these show through the animal. The other pair of lateral setae, L_1, is located one near each lateral margin of the mite opposite the third and fourth pairs of legs. In *S. scabiei* var. *equi* the last mentioned seta is ventral in position. The setae D_2-a, D_3, D_4, and D_5, are not present in *S. scabiei* var. *equi* (Buxton, 1921).

THE VENTRAL SURFACE

The anterior part of the ventral surface is somewhat flattened, but in the gravid female may be swollen from the region of the camerostome posteriorly. If the number of embryos within is not too large, the ventral surface may not be swollen anterior to the "genital operculum" which is probably the most prominent feature of the ventral surface. The term genital operculum, was applied by Buxton in the case of *S. scabiei* var. *equi* to a transverse flap which covers the tocostome or birth pore. A structure corresponding to the genital operculum is found in *C. mutans*. The heavily chitinized, thickened lips of the tocostome located in the midlongitudinal line in *S. scabiei* and which I have readily recognized in the sarcopt of the ferret, could not be found in *C. mutans*. In connection with the tocostome of the sarcopt of the horse Buxton writes: "In specimens which have been killed before oviposition, the lips (birth pores) may be seen widely separated to allow for the passage of the egg. There is, therefore, no doubt at all that this orifice is the tocostome, that is to say, the birth opening or passage through which the egg is laid." In *C. mutans*

sections through the area of the operculum show a shallow, wide invagination in the same position as that of the tocostome of *S. scabiei* var. *equi*. This is undoubtedly the birth pore of *C. mutans*. Freshly laid eggs, containing mature larvae, have been observed in the position of the tocostome. These observations were made on individual females placed in culture slides.

The ventral surface shows a varying number of annulations from the region of the cephalic end of the genital operculum to the caudal end of the body. The caudal eight or ten are only partial rings, each one being made up of several plates. Several of the other lines on the ventral surface are broken. Annulations about the legs are especially difficult to find. The regions just back of the first and the third pairs of legs and immediately anterior to the genital operculum seem to be devoid of annulations.

Setae: The setae of the ventral surface are not numerous. They are visible under a magnification of about 400. The most anterior pair of setae, V_1, is located between the first and the second epimeres (Figure 2, Plate I) nearer the latter and some distance from the proximal margin of the epimeres. The second ventrals, V_2, are located anterior and lateral to the fourth epimeres. Towards the midlongitudinal line from the third, or more often from the base of the fourth epimeres are found three pairs of setae, V_4, V_5, and V_6, arranged in the form of a triangle with the setae distant from one another by the width of about five abdominal annulations. These were first observed under oil immersion, but are indistinctly visible under high dry. Curiously enough, one member of a pair may not be in the same ring as its mate of the opposite side. Setae similar to these are figured by Ehlers (1873) for "*Dermatoryctes*" (*Cnemidocoptes*) *fossor*. Near the posterior end of the mite and laterad to the anus a single pair of setae, V_7, is found. These are the longest setae on the ventral surface. It may be that one of the last four setae is comparable to the third ventral of Buxton (1921).

THE LEGS AND THEIR ATTACHMENTS

The Epimeres: There are four pairs of epimeres (e I-IV, Figures 1–4, Plate II) which serve as points of attachment for the legs and for some of the leg muscles. Buxton, in describing these structures for *S. scabiei* var. *equi* states: "One is tempted to think of them as ridges for the attachment of muscles, as apodemes in fact; I am not prepared to say that they never fulfill this function, but it is certainly not their prime function." In *C. mutans* the epimeres are darker thickenings of the cuticula. Attached to each epimere is a delicate part which appears membranous. These are shown in Figures 1–4, Plate II. In sodium hydroxide treated specimens they are distinct and appear as superficial thickenings, but when the muscles are intact they cannot be distinctly made out. In those cases where they are clear the muscles usually appear to attach dorsad to them on the epimeres or at the point where the membrane joins the epimere. The membranes could not be differentiated in sections.

In the adult female the epimeres of the first and second legs are quite alike. From the point of union with the legs which are lateral

in position on the gravid female, they extend in a broad curve ventrad, then posteriorly towards the median line of the body. They never approximate one another on the median line. In some stained specimens slight thickenings of chitin, continuations anteriorly of the second epimeres, extend along the lateral margins of the genital operculum. The anterior part of the fork of the second epimere is much longer than that of the first epimere.

The third and fourth epimeres (e III and IV, Figures 3 and 4, Plate II) are quite alike. They are distinctly ventral in position and from the fork extend cephalad and mesad to a position which makes a wide curve with the epimeres of the first two pairs of legs and the lateral margins of the genital operculum. They are not nearly as large as are those of the first two pairs of legs. Each of the third epimeres (e III) bears a pronounced spur at the distal end. This spur is just proximad to the articular surface and does not form a part of it. It does, however, serve for the attachment of muscles. The fourth epimere, e IV, bears a spur at its anterior proximal end. This serves for the attachment of a large muscle which extends to the third pair of legs.

The Legs: The legs of the female are short and thick. The segmentation is not nearly as distinct as in the legs of the larvae and males. All the legs are apparently five-segmented, but the separation points between the fourth and fifth joints of the fourth pair of legs is incomplete and is very indistinct in the third pair. The structure of the legs is more easily studied from the ventral than from the dorsal surface. However, when the specimens are cleared and mounted they are easier to study from the dorsal surface. The first and second pairs of legs are best studied in lateral view. Specimens treated with sodium hydroxide, washed in acetic acid followed by water and then lightly stained with eosin, carmine, or picric acid, and mounted in euparal proved the best for the study of the structure of chitinous parts.

In the adult female the first two pairs of legs appear to extend dorsally rather than ventrally as in immature forms and in the males. This is due to the swollen condition of the gravid female and to the enlargement in the region of the genital operculum. This no doubt comes about because the dorsum is more rigid owing to the longitudinal and transverse bars and to the sheetlike dorsal longitudinal muscles. The basal joints of the first two pairs of legs are well set into invaginations of the lateral body wall. Sometimes the entire first joint and a part of the second joint are within this pit, but often the anterior part of the first joint extends beyond its margin. The hind legs are usually not so deeply inserted. The segments of the legs are distinguishable from one another chiefly by the chitinous ridges making up the segment. With few exceptions which are discussed, the following description based upon the first two pairs of legs is applicable to the other legs.

The first and second pairs of legs are nearly alike. In ventral view there seems to be no difference between them except the slight difference in size, the first pair being slightly larger than the second.

The first pair measure about 0.07 mm. in length and the second pair 0.06 mm. (These measurements are probably excessive as they were made on specimens which had been treated with potassium hydroxide). It is believed, however, that the relative sizes have not been altered. The first or proximal segment has a basal rounded projection which as seen ventrally fits into the acetabulum-like part of the epimere. The distal margin of the heavier chitinized band is decidedly concave in this region. A short pedal seta, P_1, is found on the chitinous band just proximad to the concavity. This seta is lacking on the fourth pair of legs. The anterior and posterior margins of the band extend farther distad than does the center region. The dorsal part of the band when viewed through the ventral surface is very narrow. In dorsal view, the band appears to be much wider (Figure 1, Plate II).

The second joint is by far the most difficult to interpret. Ventrally the chitinous band is somewhat "T-shaped" agreeing in this repect with a similar structure described for *Sarcoptes* (Buxton 1921). On the second joint in the sarcopt of the ferret (*Putorius sp.*) I have found a spur as described for *S. scabiei* var. *equi* by Buxton (1921). This spur is not present in *C. mutans*. In one specimen of *C. mutans* a very slight projection with the appearance of a rudimentary spine was found on the second joint, but was not in exactly the same position as the above-mentioned spur. The dorsal surface seems to consist of two chitinous bands, one near the distal edge of the segment and one near the proximal margin, leaving a large slightly oval space between. The distal band is much thinner than the proximal and its posterior half is much more delicate than the anterior half. It may be that a similar arrangement in the genus *Sarcoptes* led to the description of the transverse band of chitin in this segment. In many specimens viewed from the dorsal position the proximal posterior margin of the second segment extends within the first segment, as is clearly indicated in the figures of the dorsal surface of the legs (Figures 1 and 3, Plate II). The distance that the second joint would extend within the first must depend upon the angle at which the leg is bent. A seta, P_2, is located near the distal part of the bar of the T on both the first and second segments, but is lacking on the last two pairs of legs.

The third joint consists of a simple ring of chitin, usually concave along the distal margin, but projecting slightly proximad near the anterior basal border. A short seta, P_3, is found on the midanterior margin of both the first and the second pairs of legs, but is lacking in the last two. This anterior region is more heavily chitinized and is partially divided at the origin of the setae. On the dorsal surface of the joint, two setae, P_4 and P_4-a, are present on the first leg, one seta, P_4 or P_4-a, is found middorsally on the second leg. The third and fourth legs lack setae in this position.

Dorsally the fourth and fifth leg segments appear more distinct than they do ventrally, as is shown in the drawings of these legs, but they are so intimately connected that they will be considered together. The first and second legs have a single seta, P_5, on the anterior surface where the fourth and fifth segments come together. Although sometimes present, this is usually lacking in the third and fourth legs.

Dorsally the first pair of legs shows two blunt setae apparently inserted, one, P_6, proximad to the other P_7, on the distal margin and anterior to the middle of the fourth segment. These are present in the same position on the second leg, while on the third and fourth legs only one blunt seta, P_6, is found. On the first and second legs a very minute seta, P_{7}-a, is placed just distad to P_7. Posterior to the blunt setae (P_6 and P_7) are two setae, P_8 and P_9, of which P_9 is the longer and is attached to the distal margin of the fourth segment; P_8 is anterior and distal to it and has its origin at the joining point of the third and fourth segments. In the first pair of legs, P_8 is blunt; in the second pair, P_8 is a fine pointed spine. On the last two pairs of legs P_8 is replaced by a long pointed spine. This is located immediately distad to the blunt seta, P_6. Ventrally the fourth and fifth segments of the first two pairs of legs bear three spines, P_{10}, P_{12}, and P_{13}. These spines are present in similar positions in the last two pairs of legs. In addition, the last two pairs of legs bear another seta, P_{11}, which arises between the claws.

In the first and second legs some variation exists in the positions of the setae, as indicated in the figures of Plate II.

The setae P_{4}-a, P_{11}, P_{12}, and P_{13} are not described by Buxton (1921) as present in *S. scabiei* var. *equi*.

The Capitulum: The interpretation of the parts making up the capitulum is a difficult task. A contemplated study of these structures in other members of the Sarcoptoidea may lead to a somewhat different interpretation of the parts.

The capitulum is between 45 and 55 microns in length, and 75 microns in width. The posterior part is covered dorsally and ventrally by a cuticular extension of the body wall (Figures 1 and 4, Plate III). Dorsally a heavier strip of chitin on each side attaches this part to the anterior margin of the dorsal horizontal bars (Figure 1, Plate I). For the sake of clearness further details are presented after a discussion of the mouth parts.

The Chelicerae: The chelicerae are located dorsally one on either side of the median longitudinal axis. Ordinarily about half of each chelicera extends anteriorly beyond the prolongation of the body, the epistome. Each chelicera is about 50 microns long, 30 microns from the dorsal to the ventral surface, and 10 to 12 microns at the point of maximum width, i.e. a short distance from the posterior end. In lateral view (Figures 2 and 3, Plate III) the chelicera is roughly oval. it is composed of a large base and a ventral movable digit (Figures 2 and 3, Plate III). Both the digit and the heavily chitinized structure of the base opposite it are dentate, but the number of teeth does not seem to be constant. Commonly there are three teeth on the base; a large hooklike tooth and one or two smaller teeth are present on the movable digit. Norner (1882) mentioned three teeth on the digit. The digit in *C. mutans*, unlike that of Sarcoptes, does not show laterad to the base of the chelicera when viewed from the dorsal surface. In dorsal view the apex of the digit may be seen to project beyond the tip of the chelicera proper. Haiduk (1909) and Norner (1882) mention the presence of small "Kieferfühler" apparently at the sides of the digits.

I have not found them either at the sides of the digits or at the sides of the chelicerae The chelicera is rounded posteriorly and not narrowed as in the case of Sarcoptes. In addition to the more heavily chitinized parts mentioned, i.e. the digit and the heavily chitinized part opposing it, we find at the posterior end two chitinous bands. (These are shown as more finely stippled areas in the diagrams of these structures.) The more heavily chitinized areas along the ventral surface of each chelicera serves for the insertion of muscles.

The Pedipalps: Lateral to the chelicerae are the pedipalps. Dorsally each pedipalp consists of a thin chitinous structure. In specimens treated with potassium hydroxide there appear three openings. The largest of these is on the median line and in shape reminds one of the late embryonic heart of the fish, with the region of the ventricle extending toward the margin. The distal opening is the smallest (Figure 1, Plate III). The median opening lies midway between the other two. Segmentation of the pedipalps is lacking, but the openings just described may indicate the position of the three segments. On this surface there are three setae, C_1, C_2, and C_5 (Figure 1, Plate III). C_1 and C_5 are stout, long setae which extend across the chelicerae. C_2 is small and short. Each of these setae probably arises from a separate segment (Figure 1, Plate III).

At the point of origin of seta C_5 there appears a distinct fold which extends slightly dorsad and caudad. This furnishes the point of attachment of muscles which retract the pedipalps.

A structure reminding one of a sense hair, visible with a 10X ocular and an oil immersion lens, is found on each pedipalp in a cephalic position. This structure is clublike and is either quite rough in outline or segmented. Figure 1, Plate IV, shows this hair in a slightly more dorsal position than that in which it is sometimes found.

Figure 6, Plate III, illustrates the chitinous internal structure of the pedipalps, with the chelicerae in position between them. The peculiar, irregular arrangement of the bands of chitin defies any rational explanation of their relation to the segments. The author believes that A represents the basal segment. The remainder is a picture puzzle for the present.

Ventrally the structures of the capitulum are quite different from any with which I am familiar. One prominent feature of this surface is a heavy chitinous band (Figure 4, Plate III) forming a lateral and anterior margin for the capitulum and continuous with the framework of the first pedipalpal segment. Attached to the inner anterior and lateral margins of the band, and covering the anterior half of the capitulum is a thin covering (Figure 4, Plate III). A pair of setae, C_4, are borne on this covering in a latero-anterior position close to the marginal band. The band itself close to this point in some specimens has a roughened surface as if for scarification of the host tissue. Extending caudally in a median longitudinal plane is a band of chitin arising from the marginal band and extending ventrad and caudad from beneath the ventral covering of the capitulum. The point of greatest depth of the capitulum is just where this band emerges from the caudal edge of the anterior covering of the capitulum (Figure 4,

Plate III). This point is the most ventral part of the capitulum. From the caudal margin of the anterior capitular covering the median longitudinal band extends caudad and dorsad and divides into two bands which surround a nearly oval opening. The bands surrounding this oval opening are probably the maxillae of Robin (1860). The posterior end of the opening is more dorsal. It is in this region that the oral cavity is found and the beginning of the pharynx is noted with its muscles attached to its dorsal surface.

In frontal sections and in some whole mounts, especially in those untreated with alkali, another median structure, diagrammed in Figure 7, Plate III, is found just dorsad to the ventral longitudinal band of chitin. It may be continuous on its dorsal surface with the median band. This structure forms a tube, wider at the posterior end, and opens into the pharynx. At its cephalic margin it flares outward on either side into a wedge-shaped chitinous structure.

The so-called "cheek-pieces" or the "joues" of Robin (Figure 1, Plate I, and Figure 2, Plate V) are considered by some authors as a part of the capitulum. In the female of *C. mutans* sectioned material and dissections indicate that they are not a part of the capitulum, but continuations of the body-wall forming the lateral walls of the camerostome. This is in agreement with Robin's description (1860). The "cheek-pieces" fit in a curve about the lateral and anteriolateral margins of the pedipalpi. In dorsal view an area somewhat granular in appearance is present near the center of each. These granulations are not the same as those in the punctate area on the dorsal surface (Figure 1, Plate I). A heavy chitinous strip from the dorsal longitudinal bar extends into each. The structures just anterior to the second pair of legs seem to be homologous to the "cheek-pieces." They are connected with the second epimeres.

THE BODY WALL

The Cuticula: A primary and a secondary cuticula are present. The primary or epidermis retains hematoxylin stain more strongly than does the secondary cuticula or dermis. In destaining, the dermis often becomes hyaline, whereas the epidermis and the nuclei of the hypodermal cells retain the stain. Often the epidermis is as thick or thicker than the dermis. The laminate nature of the dermis can be made out with difficulty. The location and number of setae on the cuticula and the cuticular thickenings have been discussed.

Hypodermis: The hypodermis is not readily made out in many adult specimens. It appears much as it does in old insects, and reminds one more of the amnion or serosa of the insect embryo than of the hypodermis as we usually know it. The photomicrograph (Figure 1, Plate V) distinctly shows the nuclei of the cells.

THE INTERNAL ORGANS

Two important systems are lacking in this mite, namely the circulatory and the respiratory.

THE DIGESTIVE SYSTEM

The Oesophagus and Pharynx (Figure 1, Plate IV): These organs are considered together, as it is impossible to state with a degree of certainty just where the pharynx ends and the oesophagus begins. In certain saggital sections the joining point of the pharynx with the oesophagus is quite definite. The pharynx is directed upward, projects caudad and then ventrad before it joins the oesophagus which is of slightly greater diameter and without the thick chitinous walls which characterize the pharynx. The anterior part of the pharynx has muscles attached to its dorsal surface (Figure 7, Plate III). But it seems certain, judging by the greater thickness of the chitin, that the pharynx extends posteriorly beyond the muscle attachment although in this region it loses its characteristic form.

The form of the pharynx seems to agree with Michael's description (1901) of the typical pharynx of the Acarina. The upper half of the tube is apparently more flexible than the lower half, and, when the pharynx is not expanded, lies in the groove of the lower half-tube. To the dorsal concave surface of the pharynx for a distance of about 30 microns, the pharyngeal muscles are attached. These by contracting draw up the roof of the pharynx, creating a vacuum into which the serum which serves as the food is sucked. Expansion of these same muscles allows the upper half-tube to fit back into the gutter of the lower half-tube and forces the food backwards into the oesophagus and then into the stomach. I have not been able to determine whether the "occlusor muscles," those muscles attached to the lateral margins of the pharynx, are present. In their place there seems to be a strip of chitin. No muscles corresponding to the constrictor muscles described for *Argas persicus* by Robinson and Davidson (1913) are present. The pharynx when closed measures about 0.015 mm. in width and slightly over 0.0017 mm. in thickness, including both chitinous walls.

The total length of the combined pharynx and oesophagus varies noticeably in different specimens. However, at least a part of this apparent variation could very well be due to slight differences in the plane of sectioning of the different individuals, since all measurements are of necessity on sectioned material. The variation in length was from 0.059 mm. to 0.119 mm. with an average of 0.090 mm. (eight specimens which permitted most accurate measurements). In unhatched larvae the oesophagus is much longer proportionately (Figure 3, Plate VI). The oesophagus is widest just where it joins the ventriculus. The variation in width is from 0.008 mm. to 0.020 mm. with an average of 0.014 mm. (eight individuals). The variation in depth is from 0.005 mm. to 0.017 mm. with an average for seven specimens of 0.012 mm. In some specimens the oesophagus curves downward towards the stomach. This curve begins at about the middle of the oesophagus and in this region there is a slight swelling so that the width here may nearly equal the width at the joining point with the ventriculus.

Where it enters the brain the oesophagus, in sectional view, appears very irregular in outline (Figure 5, Plate VI). In more caudal sections the sectional outline is more regular. The chitinous intima becomes thinner and appears as an extremely thin covering over the epithelial

cells. The epithelial cells are quite variable in size. Some of them project towards the lumen. Outside the epithelial layer is a layer which for the most part is thicker than the chitinous intima. This is probably a layer of muscle, but it is so thin that it is impossible to be certain as to its nature. The fact that, in many longitudinal sections, food is found in the oesophagus some distance from the stomach indicates that if there is a muscular layer it is not strong enough to rapidly force the food into the ventriculus. The cells at the posterior end of the oesophagus project slightly into the anterior end of the stomach. In one case they extended for a distance of about 0.004 mm. (Figure 5, Plate IV). With the exception of these epithelial cells located at the joining point of the oesophagus and ventriculus, there are no structures which could prevent regurgitation. These cells are larger than those lining the anterior part of the oesophagus.

The Ventriculus: The ventriculus (stomach) is the largest structure within the body of the adult mite. In saggital section it is pear-shaped with the oesophagus a somewhat eccentric stem. Variations in the size and shape are noticeable and do not depend entirely on the amount of food present at the time of fixation. The stomach varies in length from 0.100 mm. to 0.173 mm., with an average of 0.136 mm. (thirteen specimens). The width varies from 0.093 mm. to 0.184 mm., with an average of 0.131 mm. (ten individuals). The depth varies from 0.064 mm. to an extreme of 0.180 mm., with an average of 0.114 mm. From these figures it will be noted that the greatest range in variation is found in the depth of the organ, the distance from the dorsal to the ventral surface. This is the measurement which one would expect to find varying most, according to the quantity of food present. In nearly all cases the depth was less than the length or the width. The measurements of the latter were quite the same, varying only in thousandths of a millimeter. All of the above measurements are for maximum dimensions of the organs in the different specimens studied. The broadest and deepest portions of the stomach are caudad to the middle, while the longest region is ventral to the median longitudinal axis. The point at which the ventriculus opens into the intestine varies extremely in different specimens. The opening which is always present is at a point between the median dorsal and the dorsocaudal positions. Norner (1882) in a study of *Dermatoryctes mutans* (probably identical with *Cnemidocoptes mutans*) considered the stomach as a blind sack. Stekhoven (1921) in a study of *Notoedres notoedres* stated that the opening into the intestine was in the middle of the hind border of the stomach through which food balls pass directly to the rectum.

Histology of the Ventriculus: The greater part of the stomach wall consists of an epithelial layer. In this layer the cell walls are not always distinct in transverse sections. In horizontal sections showing surface views of the cells, the walls are more distinct. The nuclei and the nucleoli of most of the epithelial cells are distinct and where the cell walls are not visible appear as rounded bodies, well separated from one another, lying in the granular cytoplasm. The outer wall of the epithelial cells seems to be continuous. This may indicate the presence of a muscular layer such as is found in ticks. This layer is extremely delicate and is continuous with, if not a part of, the outer delicate

covering of the ventriculus. The latter layer is spoken of as the "tunica propria."

The Intestine: Where it leaves the ventriculus (Figure 1, Plate IV) the intestine projects dorsad, then bends ventrad until it rests tightly against the ventriculus. At the same time it extends posteriorly. In those cases where the intestine leaves the posterior angle of the ventriculus the intestine also bends ventrad. In any case, it often reaches a point somewhat less than half way between the dorsal and ventral surfaces, then projects caudally and after one or two short curves extends almost in a straight line to the anal opening. The width of the opening leading from the stomach into the intestine varies, but is usually narrower than other parts of the intestine. The opening into the intestine varies from 0.006 mm. to 0.032 mm., with an average of 0.018 mm. (six specimens); the variation in depth is 0.007 mm. to 0.041 mm. with an average of 0.020 mm. (seven specimens). In several cases the opening into the intestine was nearly closed due to the larger cells which extend from the anterior edge of the intestine into the posterior part of the ventriculus. In two cases I have found them filling about one-third of the lumen of the ventriculus, forming a mass of cells 0.051 mm. in width, 0.032 mm. in length and 0.035 mm. in depth. These cells may have a distinct role in digestion.

In some specimens the appearance of the middle region of the intestine is much altered (Figure 6, Plate IV). It widens out, but the lumen does not increase due to the large cells within. In a few specimens the cells were so large as to nearly close the tube, thus giving the semblance of a valve. Inasmuch as these cells occur at the beginning of the chitinized area, between the areas spoken of as the colon and the rectum by Michael, the question naturally arises as to whether or not they take the place of Malpighian tubules in insects. They are in the same relative position as the excretory bodies described for the *Tyroglyphidae* and *Gamasidae* by Michael and Nalepa. Michael states that in the *Tyroglyphidae* they are delicate and evidently not functional and more rudimentary or recent in development than in *Gamasus*, in which they are large and conspicuous and discharge a quantity of white opaque excretory matter. Crystals and concretions are not found in the body nor is there a large excretory organ as described for the *Trombididae* and *Hydrachnidae*.

The rectum (Figure 9, Plate VI; Figures 1 and 6, Plate IV) consists of a nearly straight tube which is heavily chitinized, the chitin becoming thinner from the outside to the origin of the colon.

THE NERVOUS SYSTEM

The central nervous system of *C. mutans* is a rather compact mass in which the so-called suboesophageal ganglion is directly ventrad to the supraoesophageal ganglion, or the brain. The connectives between these structures are very broad and heavy, so that there is little differentiation between the parts of the ganglionic mass. The brain is ordinarily broader and shorter than the suboesophageal ganglion, which often extends caudad beneath the ventriculus (Figure 4, Plate VI). In many cases the arrangement reminds one of a retort with a quite

heavy stem which gradually tapers to a point. Again the size varies greatly depending to a large extent on the great variation in the size of the adults. The variation in length of the nerve mass is from 0.035 mm. to 0.091 mm.; the average for seven specimens was 0.059 mm.; variation in width was from 0.036 mm. to 0.090 mm. with an average for seven of 0.028 mm.; the variation in depth was from 0.028 mm. to 0.069 mm. with an average of 0.050 mm.

The cavity through which the oesophagus passes through the center of the brain is little larger than the oesophagus (Figures 5 and 6, Plate VI).

In a few slides some of the larger nerves leading from the central ganglionic mass show clearly. Sections caudal to the middle of the nerve mass show nerve fibers leading to the muscles and body wall (Figure 6, Plate V). The area bordering on the oesophagus and making up about half of the diameter of the ganglia lacks the large distinct cells and appears homogenous in nature. This is the "punkt" substance or neurophile. There are several layers of cells making up the nerve mass outside of the "punkt" substance. This is in agreement with Hilton's (1933) discussion of the nervous system of *Acarina*.

GLANDS

A pair of large pyriform glandlike organs, one on either side, is present in the anterior part of the body (Figures 10, 4 and 2, Plate VI; Figure 1, Plate V). They extend from the nerve ganglion anteriorly into the pedipalps. They appear to pass out of the pedipalps towards the midsaggital line of the mite. Figure 1, Plate V shows, beneath the pharyngeal tube, a concentration of the granular material where I believe a duct must lead toward the median line. The ducts may unite near the point diagrammed. I was unable to determine whether they enter the pharyngeal tube or not. They may pass beneath the tube and open near the tip of the capitulum. Stanley (1931) in *Laeleps echidninus* found that the salivary duct crossed through the substance of the median wall of each palpal stipe, entered the stylus and eventually opened to the outside through a small pore.

The palpal glands are about 0.09 mm. in length and as much as 0.076 mm. in width. In outline they are quite regular. The cells making up the outer walls are best observed on the ventral or dorsal surface of the gland. They vary in size, depending upon the stage of secretion. Granules are distinct in the largest of these cells. A nucleus with a large nucleolus is usually visible. In some cells vacuoles appear. In Figure 1, Plate V, the border layer is represented as cellular although very few cells can be observed.

Towards the center of the gland from the peripheral layer the organ is solidly filled with a rather homogenous, finely granular material arranged in part in the form of a delicate reticulum. A few bodies which are probably nuclei, but which remind one more of gregarine parasites are found throughout the glands. The nucleus is usually elliptical and larger than the nuclei in the peripheral cells. The nuclear membrane is clear and like a cyst wall in appearance. Within each nucleus the nucleolus is very darkly stained with iron haematoxylin.

In some of the nuclei, granules, similar to those filling most of the glands are present.

These glands are probably homologous with the "palpal organs" described for *Thyas petrophilus* and may be homologous to the salivary glands in *Laelaps echidninus*. Their function is unknown. Their appearance is much like that of the so-called venom secreting cells of the salivary glands of *Ixodes hexagonus* by Bonnet (1906). The nuclei more closely resemble those figured by Phisalis (1922) after Blanchard than those represented by Blanchard (1909) after Bonnet. Robinson and Davidson (1913) discuss this part of the gland as "Type II." In *C. mutans* the glands may be salivary in function, but from their general resemblance to poison glands in vertebrates and to these so-called venom cells of Bonnet it is thought that they may produce an irritant which causes a serous exudation. This serous exudate together with tiny fragments of epidermis probably serves as the food of the mite. I have not observed blood cells within the alimentary tract. Very often beneath the scales, where the mites have come in contact with the host tissues, large erythematous blotches appear. The mites are not in contact with the blood. The hardened exudate beneath the scale loosens the scale. Stekhoven (1921) found that *N. notoedres* took in blood, but the chief food was the epithelial tissue of the host.

THE REPRODUCTIVE SYSTEM

The ovaries are two ovoid or round structures located close together in the ventral posterior part of the mite. The average diameter of the ovary (fourteen specimens) is 0.044 mm., with a variation from 0.034 to 0.059 mm. The average length varies from the average width in thousandths of a millimeter. The immature ova (Figures 2 and 7, Plate VI) probably mainly first oocytes and secondary oogonia—the chromosome arrangement is not distinct enough to determine this—are more numerous in the posterior-dorsal part of the ovary. I have found up to forty of these cells, each with a distinctly stained nucleus. In some of the larger cells toward the anterior part of the ovary, the nuclei are much larger and the chromatin appears more dense around the periphery. The structure of the fixed and stained ovary appears somewhat alveolar, especially near the center and toward the anterior part of the ovary.

The oviducts have their origin at the anterior end of the ovaries and a short distance from the ovaries unite to form a uterus (Figure 8, Plate VI). This structure seems to be made up of dense tissue which is capable of much expansion, thus permitting the developing embryos to be located in any part of the body not occupied by other organs. Sometimes the stomach is pushed entirely out of its normal position and its ordinary shape. (I have removed seven large embryos from a single female.) The uteruslike structure terminates in a tube heavily lined with chitin. This birth tube (Figures 7, 10 and 4, Plate VI) opens exteriorly through the birth pore located on the ventral surface between the second and third pairs of legs (Figure 2, Plate I).

The Seminal Receptacle (Spermatheca): As already stated, the opening of the sperm receptacle is anterior and to the left of the anal

opening. It is believed that the sperms are introduced by the male through this opening. (Copulation has not been observed in this species; in *P. communis* and in *O. cynotis* the male copulatory organ is inserted into the copulatory pore.) In *Cnemidocoptes* no distinct papilla exists as in *Sarcoptes*, but a rounded or slightly oval chitinous plate is found. A chitinous copulatory tube arises at the posterior median margin of this plate and extends inward to the seminal receptacle. The cells along the tube increase in size before the region of chitinization is passed. The seminal receptacle (Figure 9, Plate VI) is not spherical as described for *Sarcoptes* by Gudden (1861). It is 0.035 mm. in length and 0.02 mm. in depth from the dorsal to the ventral surface. The only figure known of the seminal receptacle of any of the *Sarcoptidae* as seen in sections is that of Stekhoven (1921) of *N. notoedres*. The seminal receptacle in *C. mutans* narrows quickly into a tube about 0.005 mm. in diameter. This curves dorsad and in Figure 9, Plate VI, passes dorsad over the rectum and then ventrad to the region of the ovaries; it may lead directly from the receptacle to the ovaries. Here it divides into two tubes which lead toward the ovaries. The connection with the ovaries is obscure.

THE MUSCULAR SYSTEM

The arrangement of the muscles was studied in toto mounts and confirmation made, where possible, by transverse, saggital, frontal, and oblique sections. The entire mounts were unstained, stained with picric acid, or for best material stained lightly with hydrochloric carmine, and mounted in gum damar. The number of muscles is not great. The size of some of them, however, makes a very accurate description impossible. Sketches of muscle groups, made as far as possible with a camera-lucida, show perhaps better than my description the location and the relationship between the different muscles.

The muscles of *C. mutans* are typical arthropod muscles. Muscles such as those of the chelicerae have greater diameter at their points of origin than at their points of insertion and the belly of the muscle is always of less diameter than one of these other points. All the muscles large enough to determine as such appear to be of the striated type.

Muscles of the Capitulum: Cheliceral muscles (Figure 2, Plate III, and Figure 2, Plate V): Two large muscles, appear to be attached to the chelicerae. Their origin is on the cephalic part of the transverse bar. One, the retractor of the chelicera, r.c.$_1$, arises near the midpoint of the transverse bar and is inserted on the basal ventral surface of the chelicera near the median line of the body. The other pair, also retractors of the chelicerae, r.c.$_2$, have their origin at a lower level on the anterior and ventral surfaces of the outer curve of the inverted T. At their origin they form a thin broad sheet. They extend cephalad and mesad, cross beneath the logitudinal bars and the flexor of the pedipalps, and attach to the caudal ventral surface of each chelicera. The tendons of the two cheliceral muscles lie one above the other or are completely fused before inserting on the chelicerae. The first mentioned of the cheliceral muscles is dorsal to the other. From the

arrangement of the cheliceral muscles it seems unlikely that they could function in any other way than as retractors or flexors. They should then pull the chelicerae backward and laterally. Extension of these muscles and probably a change in the shape of the camerostome due to internal pressure within the mite resulting from muscular contraction and movement of the blood, force the chelicerae forward with the apices close together.

Within the chelicerae themselves there are two sets of muscles. Both of these sets are attached to the digit of the chelicera. The adductor, a.d., arises as two sheets of muscle attached to the dorsal posterior chitin of the chelicera and is inserted at the posterior end of the chelicera between the two layers of the adductor and ventral to this muscle. Insertion is at the midventral point of the digit. The adductor muscle serves to close the digit against the chelicera, the retractor to separate them. The teeth on the base and on the digit lacerate the epithelial tissue to produce a serous exudate.

The flexor muscles of the pedipalps, f. pd. (Figure 2, Plate V) have their origin on the anterior margin of the transverse bar, extend parallel to the inner muscles of the chelicerae, r.c.$_1$, and insert near the caudal median line of each pedipalp on the dorsal surface on the saclike fold of chitin already described. The pedipalps are not well supplied with muscle. Extending from the lateral basal part of the first segment there is a broad muscle, pd. m., which extends anteriorly and toward the median line. It reaches the apical segment of the pedipalp. In frontal sections this one large muscle—it may be considered as a group of muscles—seems to be the only one present. In cleared whole mounts another muscle, running transversely from the base of the first chitinous loop to the tip, may be observed. This may be a continuation of the previously mentioned muscle, but close observation leads the author to believe it is distinct.

From the dorsal surface, anterior to the transverse bar, may be observed two pairs of muscles (Figure 2, Plate V) which serve as extensors of the first and second pairs of legs. The muscle, 2nd ex., arises from the ventral surface of the transverse bar and the dorsal chitinous body wall. It is inserted on the epimere of the second pair of legs near the articular surface. The first extensor muscle, 1st ex., arises along the ventral margin of the dorsal longitudinal bar, extends along the ventral surface of the bar, and is attached to the first epimere near the articular surface.

Attached to the caudal margin of the transverse bar are two pairs of rather broad flat muscles, the longitudinal dorsals, l.d.$_1$ and $_2$ (Figure 2, Plate V). The median pair is attached directly caudad to the base of the longitudinal bars, and the second, l.d.$_2$, just laterad to these on the outer angle of the inverted T. Their points of insertion, which are along the dorsal and lateral walls of the notogaster midway between the transverse bar and the caudal end of the animal, may be several times as broad as the points of origin.

Muscles beyond the middle of the notogaster (Figure 2, Plate V): Near the posterior end of the mite there are several sets of muscles visible through the dorsal wall. The most caudal pair, the anals, a., consist of rather narrow muscles. Their origin is on the chitinous body wall

laterad to the longest pair of setae, A_2; insertion is on a slight chitinous projection near the anal aperture. Ventral and anterior to this pair is a much broader pair of muscles, the rectal muscles, r. Their origin is on the lateral body wall and insertion is on the wall of the rectum. It seems likely that these two sets of muscles serve as the anal sphincters. Anterior to these are two pairs of posterior dorsoventral muscles, post. d–v.$_1$ and $_2$. Laterad of these there are two other pairs of dorsolateral-ventrals, d–l–v.$_1$ and $_2$. These latter arise from the dorsal body wall and are inserted on the lateral-ventral margin of the body. Anterior to these are two more sets of muscles parallel to one another, d–l–v.$_3$ and d–l–v.$_4$. Dorsally these are attached close to the large longitudinal dorsal muscles which extend from the dorsal transverse bar. Cephalad from the last pair of dorsolateral-ventrals and midway between the lateral margin of these and the longitudinal dorsals are found two sets of median dorsoventrals, med. d–v.

A pair of lateral longitudinal muscles, 1–1.$_1$, are attached to the lateral wall of the mite at the point of attachment of the cephalic set of the dorsolateral-ventrals at the point of lateral indentation of the notogaster and extend anteriorly to a point midway between the second and third pairs of legs. From the anterior point of attachment of this pair of muscles another pair of lateral longitudinals, 1–1.$_2$, extends forward to the region of the second pair of legs. Two pairs of small muscles, the anterior dorsoventrals, ant. d–v.$_1$ and $_2$, are found just laterad to the tips of the dorsal transverse bar.

Muscles Visible from the Ventral Surface: There are not many muscles visible on the ventral surface which have not been described for the dorsal or which are not concerned directly with the movement of the legs.

The largest ventral set, 1st V, is a pair of muscles which are attached to the median surface of the cuticular ridge extending between the epimeres of the second and third pairs of legs or are attached opposite the base of the second epimere. These muscles spread out fanlike posteriorly and insert on the ventral body wall at a point just caudad to the fourth pair of legs midway between the legs and the midsaggital plane of the body. A pair of much smaller muscles, the genital opercular muscles, g.o.m. (Figure 3, Plate V), arises on the cuticular ridge just anterior or at the point of attachment of the muscles, 1st V. Insertion is on the upper lip of the genital operculum laterad to the median line. They probably function in the opening and closing of the genital operculum.

Leg Muscles: Some of the muscles are thin and sheetlike so that when one muscle overlies another it is not always possible to find the points of origin and of insertion.

Attached to the ventral wall of the mite just ventrad of the longest ventral muscles, 1st V, is a fan-shaped muscle, the fourth flexor, 4th f. Its insertion is on the mesal angle of the first joint of the fourth leg. With their points of origin on the posterior margin of the fourth epimere three muscles, the fourth epimerals, 4th e., extend to the second joint of the fourth leg and are inserted apparently on the first ventral bar of the second joint. The distal of the three muscles proximal to the

first joint of the leg, is ventral to the other two. The longest muscle, the fourth extensor, 4th ex., attached to the fourth legs, has its origin on the mesal surface of the cuticular ridge between the epimeres of the second and third pairs of legs and on the proximal margin of the second epimere. This muscle extends dorsad to the acetabulum-like part of the fourth epimere, dorsad to the proximal part of the first joint and is attached to the first dorsal bar of the second joint and to the ental dorsal surface of the first joint.

Within the legs themselves there seem to be but two points of origin for the muscles. One is near the anterior ental surface at the base of the first joint. A muscle from this region projects posteriorly to the second joint where it is attached within the broadened part of the posterior band. The second point of origin is the proximal band of the two bands of the second joint. From this a muscle sheet of several muscle bundles extends posteriorly and distally. It is inserted at the posterior points of segments two, three, and four. The only other muscle, the third flexor, 3rd f., attached to the fourth pair of legs arises as a broad sheet on the anterior surface and the spur of the fourth epimere. It is inserted on the mesal surface of the basal segment of the third pair of legs.

The other muscles of the third legs, the third epimerals, 3rd $e._1$, have their origin on the posterior margin of the third epimere. The ventral of these extends to the second leg joint as in the case of the fourth leg. But a more dorsal and a longer muscle, the third extensor, 3rd ex., has its origin at the very tip of the third epimere and on the cuticular ridge between the second and third epimeres partly posterior and ventral to the fourth extensor. This muscle is inserted on the ental surface of the anterior part of the first leg segment. The muscles within the third leg seem not to differ from those of the fourth leg.

The muscles of the first and second pairs of legs are best observed in lateral view and are figured from this surface (Figure 4, Plate V). The second flexor, 2nd f., seems to differ most from the other muscles. It has its origin on the cuticular ridge, the continuation dorsally of the anterior spur at the base of the third leg. This muscle, when flexed, curves twice before inserting on the distal anterior angle of the first joint. Attached to the spur of the third epimere and on the anterior surface of the epimere itself is a broad sheet made up of several flexor muscles, 2nd $f._2$, which are inserted on the anterior ental surface of the first joint. On the posterior surface of the second epimere are muscles which are inserted near the basal and posterior part of the second joint. In addition to the muscles just described as entering the leg and to the two sets of internal muscles which are similar to those of the third and fourth legs, one finds an exceedingly thin ventral muscle whose origin is near the base of the first joint and which extends to the tip of the leg. It could not be determined whether this muscle is attached directly to the claw or not.

Four distinct sets of muscles are seen to extend to the first legs. The two sets nearest to the surface are inserted on the cuticular ridge, c.r. (Figure 4, Plate V), just posterior to the point where the first joint of the leg fits into the groove of the epimere of that leg. One

set, the first flexors, 1st $f._1$, of two, sometimes apparently three, muscles extend fanlike posteriorly and has its origin along the center of the anterior margin of the second epimere. The other set, the first epimerals, 1st $e._1$, extends ventrally and originates along the posterior border of the first epimere. With its origin immediately dorsad to this muscle set, but not reaching to the distal third of the first epimere, a sheet of three muscles, 1st $e._2$, the proximal one dorsal to the other two as in the fourth pair of legs, extends to the basal posterior part of the second segment. The fourth set of flexor muscles, 1st $f._2$, is attached distally to the middle of the anterior surface of the second epimere, passed dorsad of the other muscles and is inserted on the inner surface of the first joint. The muscles of the first joint itself seem to be heavier and not sheetlike as in the other legs. They extend from the base of the joint to the posterior surface of the second joint as in the other legs. The other muscles are similar to those described for the third and fourth legs.

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EXPLANATION OF PLATES

Plate I

Fig. 1. Dorsal view of *Cnemidocoptes mutans*.
Fig. 2. Ventral view. A_1 and $_2$, anal setae; ch. p., "cheek piece;" c. p., copulatory pore; D_2, $_{2-}$a, $_3$, $_4$, $_5$, and L_2, dorsal setae; D. L. B., dorsal longitudinal bar; g. o., genital operculum; L_1, lateral seta; P. A., punctate area; Pd., pedipalp; tr. b., transverse bar; V_1, $_2$, $_{4-7}$, ventral setae; 1–4, legs. (The chelicerae are not shown in Figure 1, but are drawn within the epistome.)

Plate II

Figs. 1–4. *Cnemidocoptes mutans*. The legs and their epimeres. 1, dorsal view of 1st and 2nd legs; 2, ventral view of 1st and 2nd legs; 3, dorsal view of 3rd and 4th legs; 4, ventral view of 3rd and 4th legs. e. I–IV, epimeres; P_{1-13}, pedal setae; Sp., spur; 1–5, leg segments.

Plate III

Figs. 1–7. The Capitulum of *Cnemidocoptes mutans*. 1, dorsal view; 2 and 3, lateral views of chelicerae; 4, ventral view of capitulum; 5, posterior and ventral view of capitulum; 6, median dorsal view of capitulum in frontal plane to show internal structure of the pedipalps; 7, pharyngeal tube and surrounding structures in dorsal view. (The pharynx is shown just anterior to the muscle attachment and because of a bend in the pharynx is shown in transverse section farther posterior. The palpal gland position is shown by the label palpal gland.) ad. d., adductor muscle of the digit; C_1, $_2$, $_4$ and $_5$, setae; Ch. chelicera; Pd., pedipalp; 1st, 2nd, and 3rd, joints of the pedipalps; r. $c._1$ and $_2$, retractor muscles of the chelicera; r. d., retractor muscle of the cheliceral digit.

Plate IV

Figs. 1–7. Alimentary tract of *Cnemidocoptes mutans*. 1, lateral view of complete alimentary tract; 2 and 3, cells of the ventriculus in surface view (2, non-secreting; 3, cells actively secreting); 4 and 5, ventricular cells and the beginning of the hind intestine to show valve; 6, longitudinal section of the rectum and part of the hind intestine to show excretory cells; 7, transverse section of the hind intestine near the region of the rectum. B. M., basement membrane; Ch. i., chitinous intima; e. epi., enteric epithelium; epi., epithelium; Exc. C., excretory cells; Int., hind intestine; n., nucleus; Oe., oesophagus; Ph., pharynx; Re., rectum; St., ventriculus (stomach); Val., valve between ventriculus and hind intestine.

Plate V

Fig. 1. Palpal glands.
Figs. 2–4. Muscles of *Cnemidocoptes mutans*. 1, longitudinal section of palpal glands (duct (d) shown at a lower level); 2, dorsal view of nymph showing muscles; 3, ventral view of the 3rd and 4th legs and a part of the ventral surface of the mite; 4, lateral view of 1st and 2nd legs with muscles. a., anal muscles;

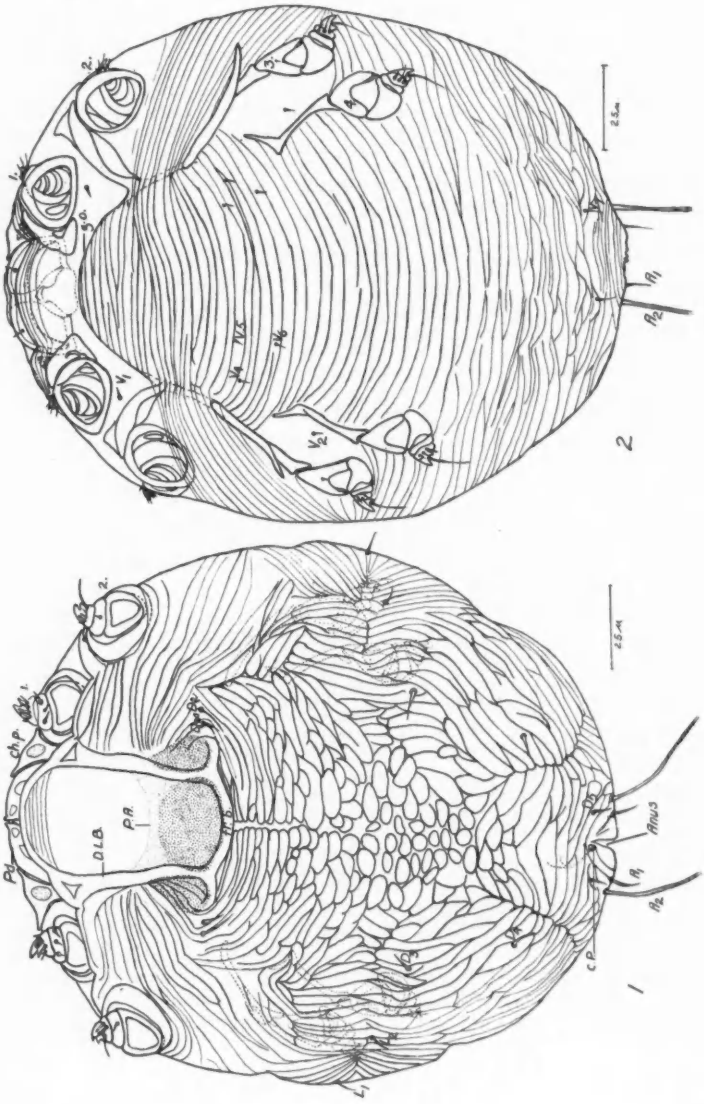
ant. d-v_1 and $_2$, anterior dorsoventral muscles; ch. p., "cheek piece;" c. r., cuticular ridge; d., duct of palpal gland; D. L. B., dorsal longitudinal bar; d-l-v_{1-4}, dorsolateral-ventral muscles; eI–IV, epimeres; 1st ex., 2nd, 3rd, and 4th ex., extensor muscles of the legs; 1st e_1 and $_2$, 2nd-4th e., epimeral muscles; 1st f.$_1$ and $_2$, 2nd f.$_1$ and $_2$, 3rd and 4th f., flexors of the legs; f. c.$_1$ and $_2$, flexors of the chelicerae; f. pd., flexors of the pedipalps; g. o., genital operculum; g. o. m., genital opercular muscle; 1-d_1 and $_2$, longitudinal dorsal muscles; 1-l_1 and $_2$, lateral longitudinal muscles; m. b., marginal band of the capitulum; med. d. v., median dorsoventrals; n., nucleus; Pd. m., muscles of the pedipalp; Ph. t., tube of the pharynx; post d-v_1 and $_2$, posterior dorsoventrals; r., rectal muscles; 1st V., ventral muscle.

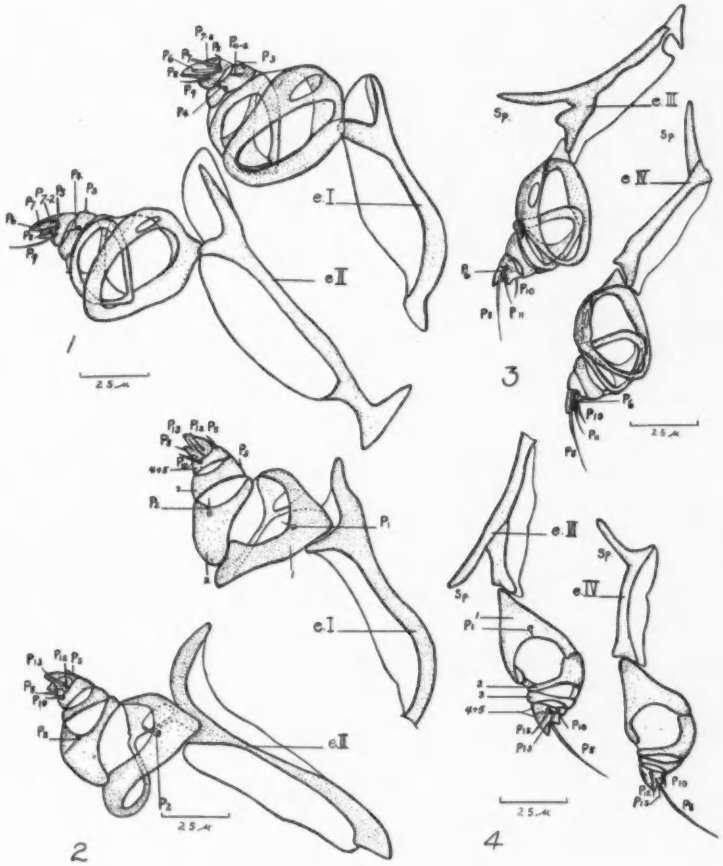
PLATE VI

Figs. 1–11. *Cnemidocoptes mutans*. 1, section of body wall; 2, midsaggital section of mite; 3, frontal section of embryo within the egg shell in the uterus of the female; 4, saggital section of mite to show the nervous system; 5, transverse section of the nerve ganglion (supraoesophageal ganglion, commissure, and suboesophageal ganglion); 6, transverse section of mite posterior to the capitulum; 7, portion of a longitudinal section to show the reproductive system; 8, transverse section of a portion of the mite to show the uterus; 9, transverse section to show the sperm receptacle and the duct leading to the ovaries; 10, transverse section just anterior to the central nerve mass to show the palpal glands with the pharynx between them; 11, fully developed embryo (larva) within the chorion immediately after the egg is deposited. b. p., birth pore; b. t., birth tube; chn., chorion; g. o., genital operculum; hyp., hypodermis; La., larva; m., muscle; n. f., nerve fiber; n. g., nerve ganglion; oe., oesophagus; ov., ovary; p. g., palpal gland; ph., pharynx; pr. cut., primary cuticula; r., rectum; sec. cut., secondary cuticula; spr. g., supra-oesophageal ganglion (brain); sp. r., sperm (seminal) receptacles; sp. r. d., duct of seminal receptacle; sub. g., suboesophageal ganglion; u., uterus: vt., ventriculus (stomach).

Anatomy of Cnemidocoptes
F. Reese Nevin

PLATE I

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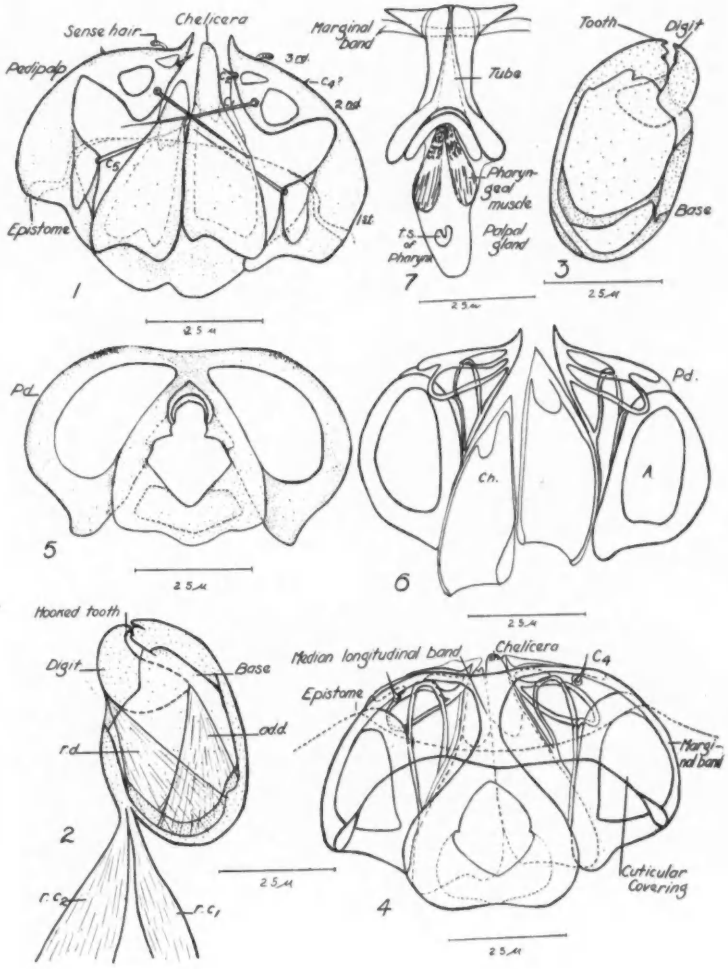
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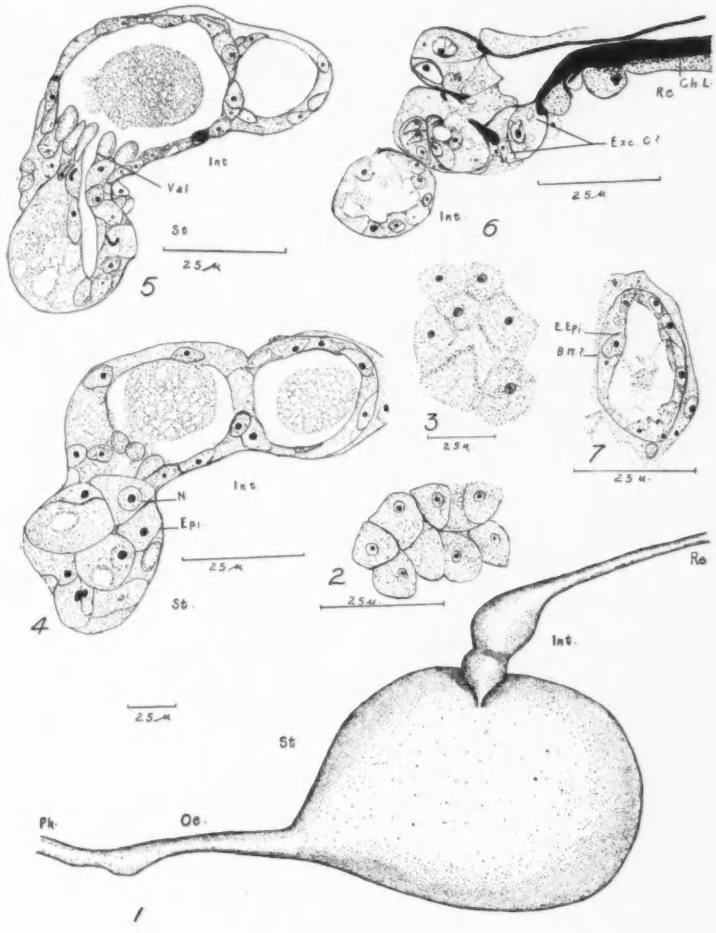
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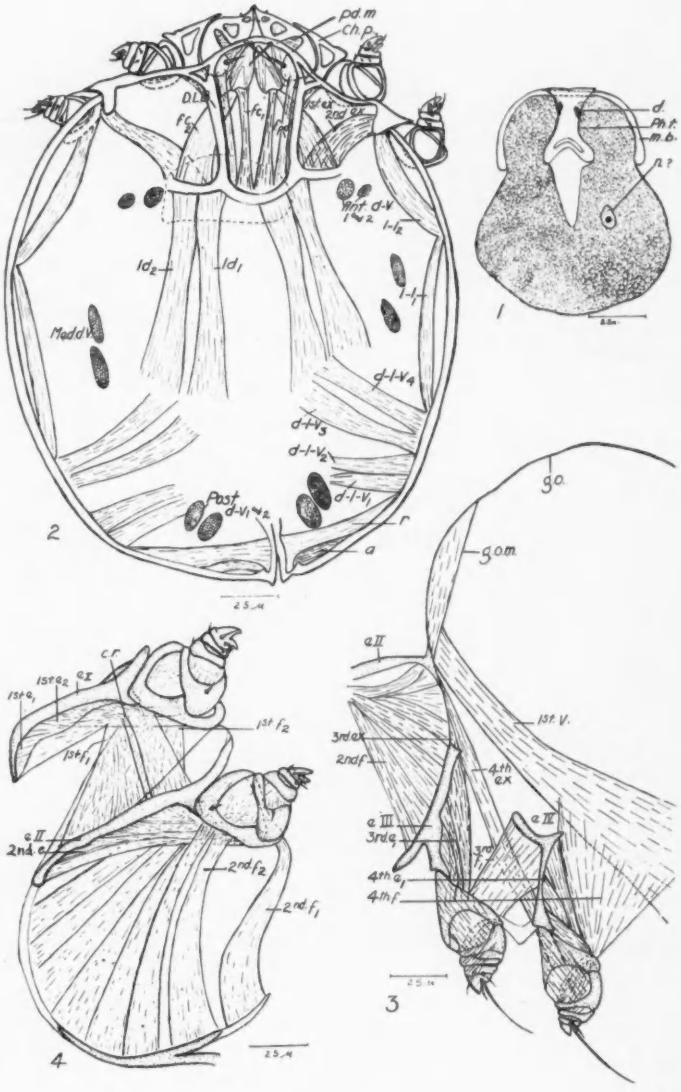
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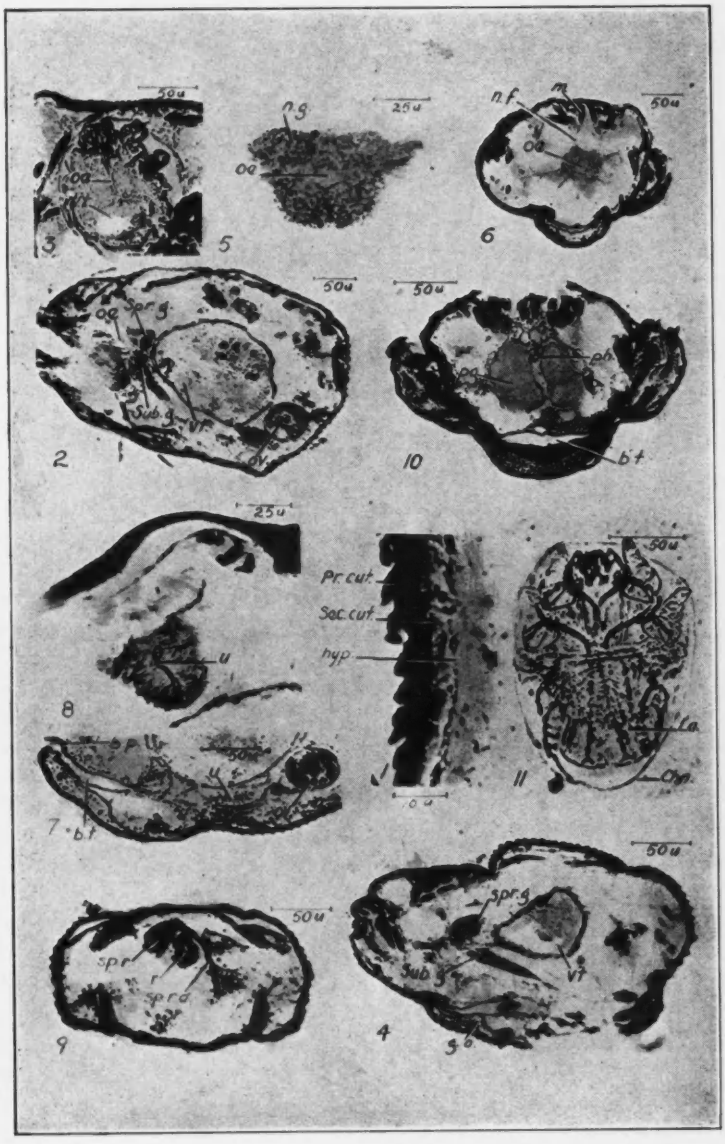
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TERMITOPHILE DISTRIBUTION AND QUANTITATIVE CHARACTERS AS INDICATORS OF PHYSIOLOGICAL SPECIATION IN BRITISH GUIANA TERMITES (Isoptera)

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During a study of the termites of the tropical rain forest of Kartabo, British Guiana, in 1919, 1920 and 1924, a collection of termitophilous Staphylinids was made from colonies determined as *Nasutitermes* (*N.*) *guayanae* (Holmgren). The fact that four species of beetles were found together in certain nests while two different species were found together in other nests excited the author's curiosity and a more thorough analysis involving a statistical study of variation in the host termites was undertaken. I am indebted to Dr. Sewall Wright for suggestions concerning statistical methods and a critical reading of the manuscript.

TERMITOPHILE DISTRIBUTION AND SPECIATION

The six species of Aleocharine Staphylinid beetles described by Mann (1923) from nests of termites determined by the author as *Nasutitermes* (*N.*) *guayanae* (Holmgren) were *Thyreoxenus major* Mann (Fig. 1), *Eburniola leucogaster* Mann (Fig. 2), *Termitophya punctata* Mann (Fig. 3), *Termitophya amica* Mann (Fig. 4), *Xenopelta cornuta* Mann (Fig. 5), and *Ceratoxenus tricornis* Mann (Fig. 6). The close similarity between the last two beetles has convinced me that they belong in the same genus, *Xenopelta*, and *Ceratoxenus* Mann is considered to be a synonym of *Xenopelta* Mann. The collection records of these species of termitophiles in termite colonies are recorded in Table I. It seems fairly clear from this distribution, that there is a differential reaction on the part of termitophiles to the host colonies which may be explained on the basis of specific differences of the host termites, although no ecological or morphological distinction of the host termites is apparent through the usual methods of field observation and taxonomic description.

The specificity of termite-termitophile relationships might be questioned. Among the termitophiles collected at Kartabo,

single Thysanuran species of *Atelura* (Folsom, 1923) were found in the nests of various species of termites ('polyxenous,' Sandground, 1929). All the species of Aleocharine Staphylinids collected at Kartabo, with the possible exception of the genus *Perinthus*, were found only with particular host species ('monoxenous,' Sandground, 1929). Mann (1923) reports *Eburniola leucogaster* from St. Joseph, Trinidad. This particular collection was from a nest of *Nasutitermes* (*N.*) *costalis* Holmgren. Careful examination seems to indicate that this termitophile is a new species of *Eburniola*, although it is quite close to *E. leucogaster* described from the nest of *N. guayanae*.

In some cases, several species of the same genus of termitophile may be found in the same colony of termites. Mann (1923) reports two species of *Spirachtha* from the nests of *Nasutitermes* (*Constrictotermes*) *cavifrons* (Holmgren) and three species of *Termitogaster* from the nests of *Nasutitermes* (*N.*) *costalis* Holmgren.

In the case of the six species of termitophiles listed in Table I, all belong to genera in which the species seem to be monoxenous, and as will be shown later, two species of termites extremely close to each other morphologically were included in the author's description of *N. guayanae* (Emerson, 1925). Each of these hosts harbors one species of *Termitophya* (Figs. 3 and 4) and one species of *Xenopelta* (Figs. 5 and 6). These termitophiles are specifically quite distinct and form the most satisfactory method for distinguishing the species of termites. No other species of *Xenopelta* are described, but another species of *Termitophya* (*T. flaviventris* Mann) has been found in the nests of *N. costalis* at Kartabo and Trinidad; *T. heyeri* Wasmann is reported from the nest of *N. fulviceps* (Silvestri) from Rio Grande do Sul; *T. holmgreni* Wasmann is reported from the nest of *N. mojosensis* (Holmgren) from Mojos, Bolivia; and *T. wasmanni* Holmgren is reported from the nests of both *N. minimus* (Holmgren) and *N. chaquimayensis* (Holmgren) from Chaquimayo, Peru. In this latter case, the description is contained in a key to the species of *Termitophya* (Wasmann and Holmgren, 1911) and I am unable to critically review the determination. This instance, if true, is an exception to the usual monoxenous relationship found among these specialized beetles.

The two species of *Eburniola* known are monoxenous.

The species of *Thyreoxenus* are each reported from a different

host: *T. parviceps* Mann is found in the nests of *N. costalis*, *T. pulchellus* Mann is found in the nests of *N. ephratae* and *T. major* Mann (Fig. 1) is found with *N. guayanae*.

All of these termitophiles seem to be symbiotic forms and should be classed as 'symphiles.' The termite workers were observed to lick *Thyreoxenus major*. This beetle moved slowly among the termites which in no case showed hostility. The

TABLE I

Records of Termitophile Species Collected in Colonies Formerly Determined as *Nasutitermes* (*N.*) *guayanae* (Holmgren)[1]

	N. guayanae								*N. similis*						
FIELD NUMBER	216	279	399	408	24.61	24.126a	Trinidad	46.47	162	169a	251	422	431	466.467	24.132a
DATE	16. VIII .20	27. VIII .20	11. X .20	13. X .20	13. III .24	20. IV .24	18. VIII .24	26. VII .26	16. VII .19	24. VII .19	22. VIII .20	15. X .20	16. X .20	4. XI .20	24. IV .24
Thyreoxenus major	x				x	x									
Eburniola leucogaster	x	x	x	x	x	x	x	x							
Termitophya amica	x	x	x	x	x		x	x							
Xenopelta cornuta			x	x	x										
Termitophya punctata										x	x	x	x	x	
Xenopelta tricornis									x		x	x	x	x	x

[1]All colonies are from Kartabo, British Guiana, except one from a Mora forest, Trinidad, British West Indies. All colonies were collected by the author except No. 46.47 collected by Lysbeth Hamilton Benkert.

remarkable glandular development of the abdomen and thorax of *Thyreoxenus* is doubtless an adaptation for the secretion of fatty exudates which enable these beetles to exploit the social behavior of their hosts. *T. parviceps* was not only seen being licked by the termites, but it was fed by regurgitation. Once this species was observed licking a termite nymph without harming the nymph, so that mutual exchange of exudates between the termitophiles and their hosts is demonstrated. One of these beetles also was seen licking another of its own

species. On several occasions *T. parviceps* was observed to bend its abdomen to one side and deposit a small drop of fluid. The termites failed to pay any attention to this action, however. *T. parviceps* was once seen (Emerson, 1929) together with other termitophilous beetles, Collembola and Acarina, migrating with its host termite (*N. costalis*) over the surface of the ground. The termite colony was invading the laboratory building at Kartabo, the reproductive pair and young also walking along

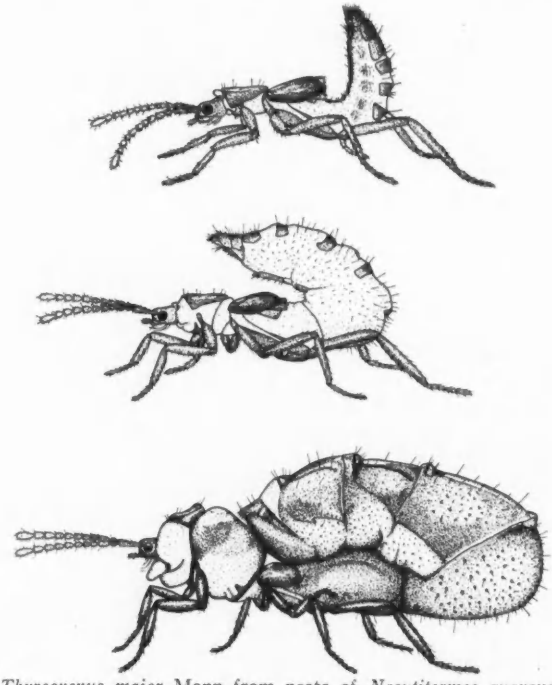

Fig. 1. *Thyreoxenus major* Mann from nests of *Nasutitermes guayanae* (24.61). Note postimaginal growth of glandular tissue.

the trail over bare ground in the early morning (7:30 a. m., June 21, 1920). The termitophiles thus show a distinctive reaction to the hosts and accompany the termites when they change the site of their nest. *T. pulchellus* Mann also walked about slowly among its host termites. Several times the abdomen was observed to rise and move forward so that the tip was well in front of the head. Once, during this action,

the beetle deposited a drop of grayish white liquid on the head of a worker and two other workers immediately licked off the liquid.

Eburniola leucogaster (Fig. 2) was the commonest termitophile in the nests of its host, often over one hundred being found in a single nest. It usually held its abdomen over its head and moved about incessantly among the termites which never exhibited hostility toward it.

Termitophya amica (Fig. 4) usually held its abdomen over its back, but occasionally it would extend the abdomen which was only slightly enlarged in the adult—an indication of only a slight development of exudate glands. The termites showed no hostility toward these beetles and my impression is that the relationship is symbiotic. The observations on *T. punctata*

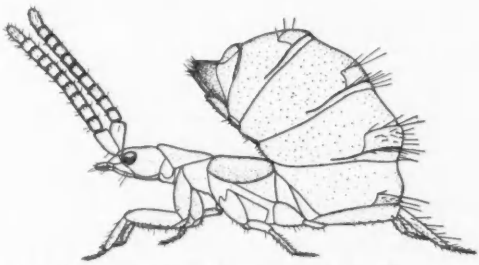

Fig. 2. *Eburniola leucogaster* Mann from nests of *Nasutitermes guayanae* (399).

(Fig. 3) and *T. flaviventris* were essentially similar to those on *T. amica*.

The two species of *Xenopelta* (Figs. 5 and 6) were both observed walking among their respective host termites, usually holding their abdomens over their backs, but occasionally extending them. Both species have similar glandular development of the abdomen and are doubtless symbiotic forms.

One nest (24.61) not only contained specimens of four species of adult termitophiles, but also contained two species of beetle larvae. A larger one with less dense pilosity was most abundant and *Thyreoxenus major* was the most abundant (108 specimens) of the adult termitophiles in this nest. It is possible that the larvae belonged to this species, but no proof of this is available. The worker termites licked and massaged these beetle larvae with their mouthparts, working gradually back to the end of the abdomen where some time was spent

licking the tip. The larvae raised the tips of their abdomens, thus facilitating the licking. Elongated eggs among the termite eggs showed similar larvae within the shell. Less elongated eggs showed a smaller species of larvae through the shell and a third type of egg, much smaller than a termite egg, might have been the egg of *Eburniola*, but in this latter

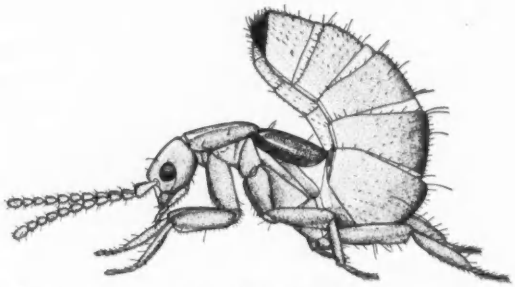

Fig. 3. *Termitophya punctata* Mann from nests of *Nasutitermes similis* (422).

case I was unable to see beetle larvae within the egg. Beetle eggs were often found in the masses of termite eggs and it seems probable that the termites treat the eggs in the same manner as their own and feed and take care of the larvae.

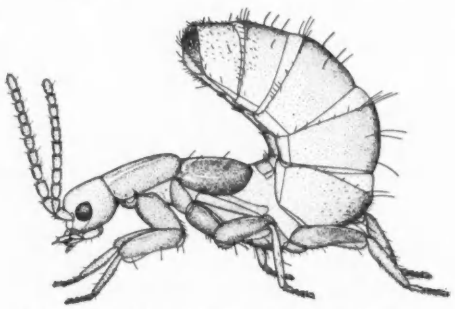

Fig. 4. *Termitophya amica* Mann from nests of *Nasutitermes guayanae* (24.61).

The development of the specialized exudate glands of the adult beetles is a postimaginal development (Fig. 1).

No observations are known to me which record the method by which the termitophiles invade the nests of their hosts. Newly mated reproductive termites with a small number of workers and soldiers were never found associated with termi-

tophiles, so it seems necessary to assume that the adult beetles fly from one nest to another before the postimaginal development of the exudate glands. It would be at this time that host selection would take place and the available data show that each species of specialized termitophile probably only invades

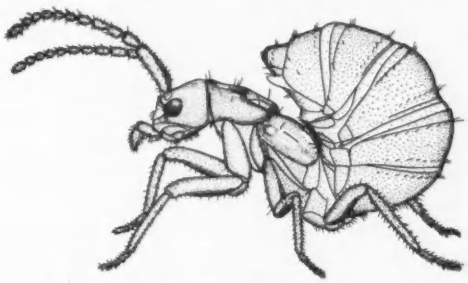

Fig. 5. *Xenopelta cornuta* Mann from nests of *Nasutitermes guayanae* (24.61).

the nests of its particular host species. It seems most probable that chemical differences in the hosts stimulate the selective response of the termitophile species, but observations and experiments dealing with this problem are lacking.

SPECIATION AMONG TERMITOPHILES

Speciation among these specialized termitophiles may have been accomplished in the following ways:

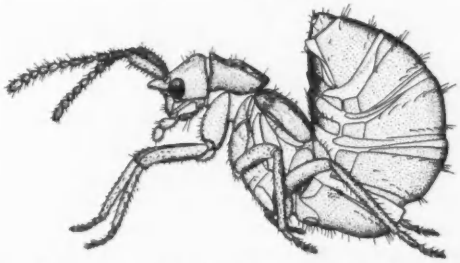

Fig. 6. *Xenopelta tricornis* (Mann) from nests of *Nasutitermes similis* (422).

1. An ancestral termite species may have harbored an ancestral termitophile species and speciation of one was associated with speciation of the other through isolation and germinal modification adapted to the social mechanisms (i. e., exudates and species recognition mechanisms). In this case the termites

may have speciated without adaptive changes, but the termitophiles would be expected to show adaptive modifications associated with the differences which would be primarily connected with the social mechanisms of the termites and their ability to react differentially to invaders.

2. Isolation of two strains of an ancestral host termite might result in isolation of the associated termitophiles through mnemonic choice during the invasion of new nests with subsequent haphazard germinal divergence. In this case it is not necessary to assume adaptive modification but merely to assume that a migrating termitophile will react specifically in its choice of nests through 'memory' of the specific attributes of that colony in which it has been raised.

3. Distribution of genetically varying termitophiles might be limited through the selection by the termites of only certain

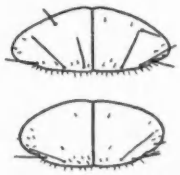

Fig. 7. Dorsal view of the pronota of two soldiers of *Nasutitermes similis* (251) showing the distribution of conspicuous bristles on the posterior margin.

termitophiles. Thus the adjustment between host and symbiont would be parallel to the adjustment of plants to soil conditions with the elimination of those seeds which happened to fall in a poor situation.

4. A termitophile species inhabiting the nest of one host species may invade the nest of a new host species and subsequent selection or habit preference might ultimately result in reproductive isolation from the original termitophile population thus giving rise to a new species through later germinal modification. A comparable incipient speciation is suggested in the case of *Ascaris lumbricoides suum* and *A. l. hominis* (Sandground, 1929). Also Baylis (1924) records closely related species of parasitic nematodes in various birds of prey or in fish-eating birds and mammals.

5. Speciation without a change or modification of the host termite might be correlated with behavior or reproductive modifications of the termitophiles which would result in reproductive isolation. In such a case two or more closely related

species of termitophiles would be found in the same termite nest and later might separate or not with subsequent speciation of the termites.

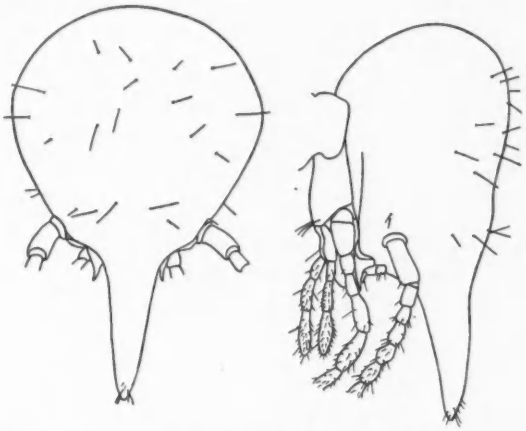

Fig. 8. Dorsal view and profile of head of large soldier (2.03 mm. head length) of *Nasutitermes guayanae* (18.IV.24).

6. Free-living ancestral species of the same genus of termitophiles may have separately invaded the nests and become adjusted to various host termites. Such a method of speciation

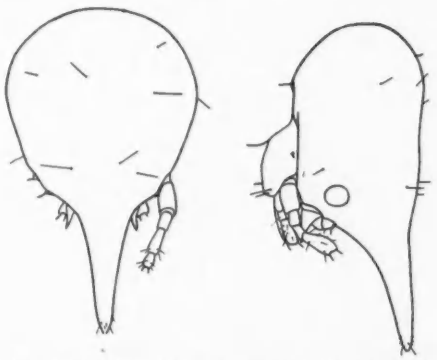

Fig. 9. Dorsal view and profile of head of small soldier (1.65 mm. head length) of *Nasutitermes guayanae* (185).

would not be expected among genera of highly specialized termitophiles without closely related free-living types and

where the relation of the species to each other and to the hosts indicates a long evolution beyond the species level within the termite nests.

The data are not conclusive in assigning one of these specia-

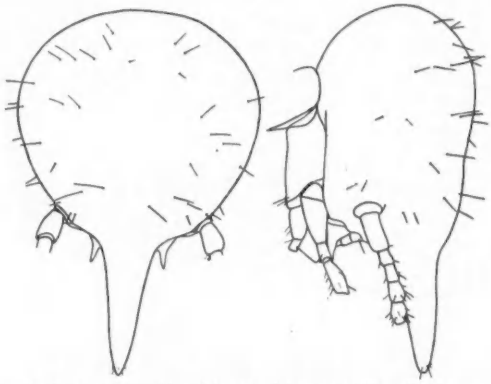

Fig. 10. Dorsal view and profile of head of large soldier (1.85 mm. head length) of *Nasutitermes similis* (422).

tion methods to the termitophiles in question. The sixth supposition seems to be ruled out, although it is to be expected that certain slightly adapted termitophiles may have evolved

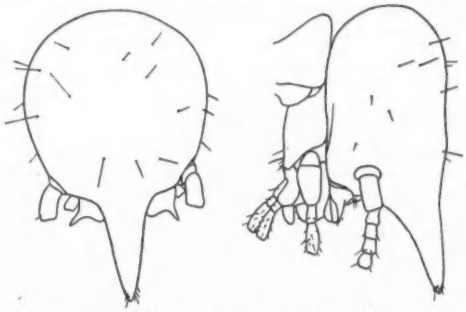

Fig. 11. Dorsal view and profile of head of small soldier (1.50 mm. head length) of *Nasutitermes similis* (467).

through such a method. The fifth supposition would only be indicated in the cases where two or more species of the same genus of termitophile were found with the same host. The fourth supposition would be indicated in the case of

termitophiles which show much closer relationship to each other than the termite species show to each other, particularly when the hosts show convergent evolution toward some particular ecological factor.

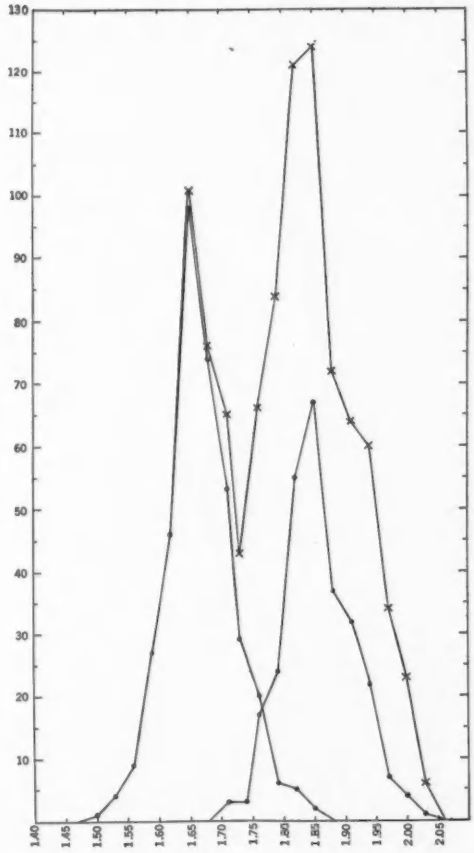

Fig. 12. Graphs of soldier head lengths. Dotted lines are frequency polygons for *Nasutitermes similis* and *N. guayanae* soldiers from several colonies containing termitophiles. Line with crosses is the bimodal frequency polygon for the entire population with and without associated termitophiles.

At present, whether the first, second or third supposition is the correct explanation of the instance reported in this paper cannot be determined. Transfaunation experiments would

give valuable clues, but as yet such experiments have not been made. Because of the close relationship of both the termitophiles and the termites from different nests, however, it would seem probable that speciation among the beetles and among the termites occurred more or less together.

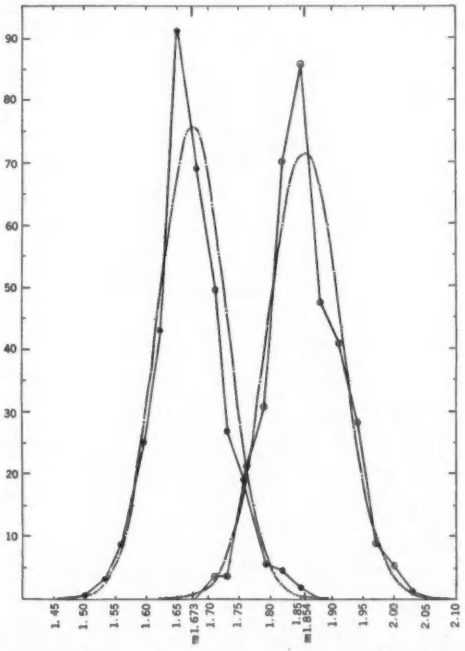

Fig. 13. Frequency polygons of soldier head lengths of *Nasutitermes similis* (solid dots) and *N. guayanae* (circles) found with termitophiles and equalized for numbers, together with the computed normal probability curves of distribution for each population.

VARIATION IN THE HOST TERMITES

The data on the termitophiles indicate that two populations of host termites are involved and with this lead, a more careful study of the termites was made.

Variation in the Soldier Caste—A careful comparison of large numbers of the two host termites failed to reveal any qualitative differences. Specific diagnosis of soldiers within the genus *Nasutitermes* usually rests upon differences in the

pilosity, shape of the head, color and size (Holmgren, 1910; Emerson, 1925).

Two characters were discovered showing significant quantitative differences, however, which correlated with the termitophile distribution. It was noted that some soldiers had one or more conspicuous bristles on the posterior margin of the pronotum while others lacked such bristles (Fig. 7). The numbers with and without such bristles are shown in Table II. In all cases, the soldiers from colonies (*N. similis*) containing *Termitophya punctata* and *Xenopelta tricornis* had a higher percentage with these bristles than without. One colony (Table II) approached equality of numbers, but the total

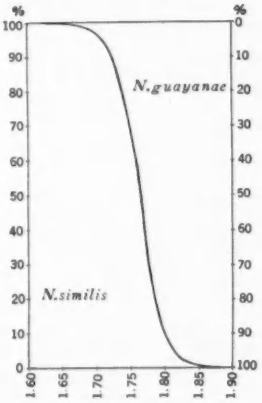

Fig. 14. Curve of species percentages of overlapping measurements of soldier head lengths computed from the normal probability curves for each population (Fig. 13).

number examined showed 328 soldiers with the posterior bristles and 89 without. This contrasts with the total of 17 soldiers with the posterior bristles and 257 without these bristles from colonies (*N. guayanae*) containing at least two of the four species of termitophiles, *Thyreoxenus major*, *Eburniola leucogaster*, *Termitophya amica* and *Xenopelta cornuta*.

Another quantitative difference between the two host termites was found in the length of the soldier head. Probably size differences could be found in the measurement of a number of other parts, but the longest measurement which could be made with considerable accuracy was the head length and this

TABLE II

VARIATION IN THE SOLDIER CAST AMONG COLONIES OF *Nasutitermes similis*, *N. guayanae*, AND *N. columbicus*[2]

Locality	Date	Coll. No.	Termitophiles Present	No. of Soldiers With Conspicuous Bristles on Posterior Part of Pronotum	No. of Soldiers Without Conspicuous Bristles on Posterior Part of Pronotum	No. of Soldiers Measured	Mode	Mean Head Length of Soldiers	Standard Error, Soldier Head Length	Standard Deviation
Nasutitermes similis:										
Kartabo	4. XI. 20	466, 467	X	51	13	62	1.65	1.627	0.006	0.0465
Kartabo	24. IV. 24	24.132a	X	97	3	100	1.65	1.661	0.004	0.0438
Kartabo	22. VIII. 20	251	X	74	66	100	1.65	1.664	0.005	0.0474
Kartabo	18. X. 20	431	X	95	5	100	1.71	1.697	0.005	0.0453
Kartabo	15. X. 20	422	X	11	2	13	1.82	1.793	0.012	0.0433
Nasutitermes guayanae:										
Kartabo	6. VIII. 19	185	.....	0	10	10	1.71	1.699	0.012	0.0372
Kurupung	XI. 22	.....	.....	0	24	26	1.73	1.760	0.009	0.0457
Surinam	27. V. 09	.....	.....	0	1	47	1.75—1.80	1.762	0.006	0.0423
Kartabo	13. X. 20	408	X	2	41	43	1.79	1.794	0.006	0.0362
Camaria	24. V. 24	.....	.....	18	82	100	1.79	1.810	0.004	0.0406
Kartabo	20. IV. 24	24.126a	X	0	38	38	1.85	1.822	0.006	0.0375
Kamakusa	X. 22	77	.....	6	94	100	1.85	1.835	0.004	0.0410
Kartabo	16. VIII. 20	216	X	2	56	55	1.82	1.851	0.007	0.0530
Kartabo	26. VII. 26	46.47	X	0	8	8	.....	1.862	0.011	0.0324
Kartabo	11. X. 20	399	X	10	78	89	1.85	1.874	0.005	0.0481
Kartabo	15. VII. 20	104	.....	4	38	42	1.88	1.876	0.007	0.0425
Trinidad	18. VIII. 24	.....	X	1	26	27	1.94	1.900	0.009	0.0478
Kartabo	27. VIII. 20	279	X	2	10	12	1.94	1.935	0.011	0.0380
Kartabo	18. IV. 24	.....	.....	18	82	100	1.94	1.956	0.004	0.0370
Total *N. similis* with	Termitophiles	.....	.....	328	89	348	1.65	1.673	0.003	0.0549
Total *N. guayanae* with	Termitophiles	.....	.....	17	257	272	1.85	1.854	0.004	0.0583
Nasutitermes columbicus:										
Frijoles	28. IV. 21	.....	.....	0	5	6	1.85	1.835	0.017	0.0413
Columbia	.....	.....	.....	0	1	1	1.76	1.760	.....	.....

[2]The colonies from Kurupung and Kamakusa were collected by Mr. Herbert Lang; colony No. 46.47 from Kartabo was collected by Mrs. Lysbeth Hamilton Benkert; the type specimen from Surinam was collected by R. Heller; all other colonies were collected by the author (except *N. columbicus*).

was deemed sufficient. The extremes for both host termites are shown in Figures 8, 9, 10 and 11, which are drawn to scale. Figure 12 shows that the soldiers of the host termite (*N. similis*) which harbored *Termitophya punctata* and *Xenopelta tricornis* varied from 1.50–1.85 mm. head length, while the other host termite (*N. guayanae*) varied from 1.71–2.03 mm. for the same measurement. The means for each colony (Table II) showed that the termites (*N. similis*) harboring *T. punctata* and *X. tricornis* varied from 1.627 mm. ± a standard error of 0.006 mm. to 1.793 ± 0.012, while the other host termites (*N. guayanae*) varied from a mean of 1.794 ± 0.006 to 1.935 ± 0.011. The frequency distribution of soldier head lengths for the entire population formerly determined as *Nasutitermes guayanae* including those colonies from which termitophiles were not collected exhibits bimodality corresponding quite well to the distribution curves of the soldier head lengths from colonies

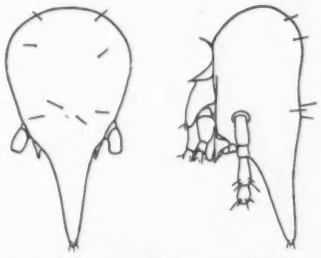

Fig. 15. Dorsal view and profile of head of dwarf soldier (1.23 mm. head length) of *Nasutitermes guayanae* from a young colony.

containing termitophiles (Fig. 12). It therefore seems reasonable to assume that we have a quantitative measurement which indicates the existence of two populations which, however, overlap in morphological characters. If the bristle count is used as a criterion, it will be noted (Table II) that one population (*N. similis*) has a variation of colony means from 1.627 ± 0.006 to 1.793 ± 0.012, while the other population (*N. guayanae*) has colony means varying from 1.699 ± 0.012 to 1.956 ± 0.004. It would thus be impossible to determine the species of certain colonies on the basis of the mean of the soldier head lengths alone, although the frequency distribution correlates with the bristle count on the posterior margin of the pronotum and with the distribution of the termitophiles and thus is a further indication that two distinct populations are involved. The

determination of individual soldiers without recourse to the associated species of termitophiles would be even more liable to error.

The theoretical overlap in individual measurement of soldier head lengths is expressed in Figure 13. The computed normal probability curves differ somewhat because the standard deviation of one population is 0.0549 and of the other population is 0.0583. The probability that any one measurement of soldier head length would belong to one population or the other is graphed (Fig. 14) from computations of the overlap of the normal probability curves. Thus, 100 per cent of the soldiers with a head length of 1.60 mm. belong to the host termite (*N. similis*) harboring *Termitophya punctata* and *Xenopelta tricornis*. Approximately 59 per cent of the soldiers

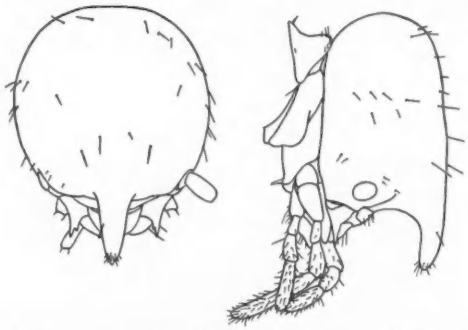

Fig. 16. Dorsal view and profile of head of intercaste soldier-worker of *Nasutitermes similis* (466).

with a head length of 1.76 mm. belong to the host (*N. similis*) harboring *T. punctata* and *X. tricornis* and 41 per cent belong to the host termite (*N. guayanae*) harboring *Thyreoxenus major* or its associated termitophiles.

Dwarf Soldiers from Young Colonies—The variations in soldiers from very young colonies were not included in the preceding account. Dwarf soldiers (Fig. 15) and workers are found in such colonies and are not to be interpreted as the result of genetic influences. Five such soldiers, constituting the total soldier population, were collected in two different young colonies. One colony contained only one soldier which had a head length of 1.23 mm. (Fig. 15). The other colony contained four soldiers, one with a head 1.26 mm. long, two with heads 1.29 mm. long and one with a head 1.32 mm. long.

In all cases, no bristles were seen on the posterior portion of the pronota indicating that the species probably is the same (*N. guayanae*) as that harboring *Thyreoxenus major* and its associated termitophiles.

Such modifications are probably the result of a small amount of food resulting from the small number of dwarf workers and the small amount of regurgitation from the young male and female. These modifications indicate that a starvation diet does not influence the caste differentiation between soldiers and workers and it also proves that size variation may be due to other than genetic causes.

Intercastes between Soldiers and Workers—Another variation not included in the preceding analysis was an intercaste between

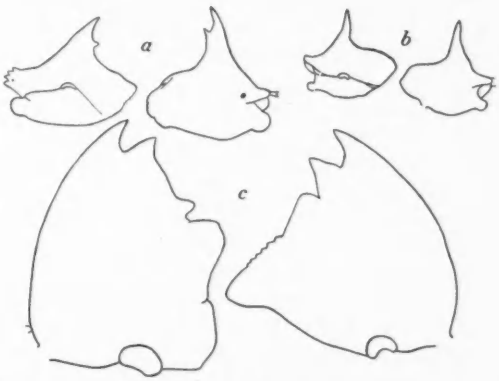

Fig. 17. Outlines of mandibles of *Nasutitermes similis* (466): a. Intercaste soldier-worker; b. Soldier; c. Worker.

a soldier and a worker (Fig. 16). Sixty-four normal soldiers and fourteen intercastes were collected from colony No. 466 (*N. similis*) from Kartabo on November 4, 1920. Measurements of the normal soldiers are included in the table and graphs. The intercastes are more soldier-like than worker-like, but most of them deviate from the soldier in having a shorter head projection and an extra tooth on each mandible (Fig. 17). Some of the specimens were more normal in shape without the extra tooth, but were abnormally small. Others had a short head projection, but were fairly normal in shape and the tooth was barely perceptible on the mandible. No indication of associated parasitism was discovered.

Intercastes between the worker and soldier are very rare and this is the only colony from which I have personally collected such forms. Snyder (1933) records the collecting of an intercaste in a nest of *Reticulitermes tibialis* Banks at Missoula, Montana, and in the same paper describes and figures an intercaste of *Nasutitermes* (*N.*) *myersi* Snyder. This latter intercaste is quite close to the worker, particularly in the mandibles and labrum which are essentially workerlike, but a distinct small head projection occurs which unmistakably is a modification toward the soldier type.

The large number of intercastes found in the Kartabo colony might suggest a genetic influence on development at the time the worker-like nymph molts into a soldier nymph. In such a case, however, one would expect to find intercaste nymphs, but of the twenty-seven nymphs with head projections which were collected in the same colony, all were of the normal soldier type. Thus it is possible that some external influence upon development occurred at one time and that these fourteen intercastes are approximately of the same age.

Whether the effect is due to some unknown environmental influence or due to a genetic influence upon development cannot be determined from the available data, but in either case the close morphological relationship between the soldier and worker castes is emphasized by such discoveries and fits the theory of the phylogenetic origin of the worker caste from the soldier caste (Emerson, 1926). I do not wholly agree with Snyder (1933), however, when he states, "The soldier develops from a worker-like form to the soldier-like form during a quiescent stage, thereby in its ontogeny expressing the phylogeny of this caste, according to Emerson's theory." If this development was an example of recapitulation, the soldier type would precede the worker type, while just the reverse is the case. I think that the worker to a certain extent is to be regarded as a neoteinic soldier type which developed through the failure of the soldier to go through its last instars.

As in the case of the dwarf soldier, the intercastes illustrate the fact that much greater variation may exist within the species than exists between closely related species. It is thus quite obvious that all attempts to define species in terms of the degree of morphological difference between individuals would be inadequate. This point has been emphasized by Sturtevant (1921) in dealing with species of *Drosophila*.

Variation in the Reproductive Caste—The numbers of reproductive forms from different colonies are not sufficient for significant statistical treatment. Three queens, a king and two winged forms from three colonies of the host termite (*N. similis*) harboring *Termitophya punctata* and *Xenopelta tricornis* were collected. Three queens and a king were collected from three colonies (*N. guayanae*) harboring *Eburniola leucogaster* and *Termitophya amica*. In addition, five queens, one king and many winged forms were collected from seven colonies which have been determined as the host (*N. guayanae*) which harbors *Thyreoxenus major* and its associated termitophiles, the determination being based upon the soldier caste without substantiating termitophile records.

No qualitative or quantitative distinction can be made which corresponds to the termitophile distribution or the associated characters of the soldiers. It is possible, however, that more material may ultimately demonstrate significant quantitative differences in the reproductive caste of the two host termites.

SPECIFIC DISTINCTION OF THE HOST TERMITES

The quantitative differences in bristle distribution and in soldier head length correlates with the distribution of the six species of termitophilous Staphylinidae and indicates that two genetically distinctive populations of termites are involved. It is possible that an environmental influence effects the morphology of the termites and is either caused by or associated with the termitophile distribution, but it seems to the author that the general evidence points to genetic differentiation of the host termites. Although the morphological criteria are extremely close, the fact that two genera of beetles have seemingly speciated in relation to these termites and that the different host populations occupy the same locality and the same ecological niche without overlapping makes it necessary to consider the termites as separate species.

Holmgren (1910, p. 254) described and figured *Nasutitermes* (=*Eutermes*) *guayanae* and gave frequency distribution of the soldier head lengths (p. 177). I have computed the mean, standard error and standard deviation from Holmgren's data (Table II). I also have a single soldier from the type colony from Upper Surinam collected May 27, 1909. This soldier

lacks conspicuous bristles on the posterior margin of the pronotum (Table II).

Unfortunately, the description and study of the soldier from the type colony do not make it possible to accurately assign one of the two species from Kartabo to *N. guayanae*. The best that can be done is to make a guess and in view of the bristle distribution I am assigning the name of *Nasutitermes* (*N.*) *guayanae* (Holmgren) to the British Guiana and Trinidad species which harbors *Thyreoxenus major* and its associated termitophiles.

The species which harbors *Termitophya punctata* and *Xenopelta tricornis* is here described as *Nasutitermes* (*N.*) *similis*, n. sp.

Nasutitermes (N.) guayanae (Holmgren)

(Figures 8 and 9.)

Eutermes guayanae Holmgren, 1910, p. 254 (soldier, worker), Text Fig. 36 (soldier).
(?) *Nasutitermes guyanae* Banks, 1918, p. 666.
Nasutitermes (*N.*) *guyanae* (in part) Emerson, 1925, p. 308 (soldier), p. 376 (imago, soldier), Text Fig. 54 (imago, soldier).
(?) *Nasutitermes guyanae* Emerson, 1929, p. 724 (biology).

Imago: Head brown to very dark brown; widely oval; clothed thickly with short hairs and longer bristles; fontanelle slit-shaped, forked at the anterior end, as long or nearly as long as the ocelli. Antennae lighter than the head, with 16 joints, the second, third and fourth joints not showing a consistent proportional relationship with each other. Eyes fairly large and somewhat close to the lower margin of the head. Ocelli of medium size, from one-fourth their length removed from the eyes to somewhat more than their length removed from the eyes. Labrum lighter than the head. Postclypeus lighter than the head, short. Pronotum yellow brown to dark brown, not as wide as the head, sides fairly straight, posterior margin emarginate, angles rounded; thickly covered with hair and longer bristles. Meso- and metanota same color as the postclypeus, posterior margins widely emarginate, angles varying from sharp to round. Abdominal tergites and sternites covered with long bristles and shorter hair, the tergites yellow brown to brown in color, the sternites fairly uniform yellow brown or with darker lateral portions. Wings brown, somewhat transparent.

MEASUREMENTS IN MILLIMETERS:

	Extremes	Average
Width of head with eyes	1.52 –1.71	1.62
Long diameter of eye	0.410–0.571	0.503
Distance of ocellus from eye	0.057–0.171	0.112
Length of ocelli	0.129–0.229	0.189
Width of pronotum	1.20 –1.48	1.35
Length of pronotum	0.64 –0.81	0.75
Length of hind tibia	1.75 –2.03	1.88
Length of anterior wing from suture	10.62 –14.29	12.28
Width of anterior wing	3.29 –4.20	3.78

Soldier (Figs. 8 and 9): Head red brown to dark brown (almost black); covered with numerous bristles, 3–6 (usually 4) at the base of the frontal projection and from 5–23 (usually about 12) on the vertex. Head somewhat egg-shaped not including the frontal projection. Top of head fairly straight in profile with an elevation at the base of the frontal projection. Antennae with 14 joints, in general the 2nd, 3d and 4th joints about equal, but varying somewhat in their proportion to one another. Frontal projection fairly large, of medium thickness, the end sometimes lighter than the rest of the head. Pronotum with a row of small hairs and a few longer bristles on the anterior margin and occasionally with one or two long bristles near the posterior margin. Abdomen somewhat lighter than the head; middle tergites with a single row of bristles on the posterior margins and entirely lacking short hairs.

MEASUREMENTS IN MILLIMETERS:

	Extremes	Average
Length of head	1.65–2.03	1.85
Width of head	0.95–1.25	1.10
Length of hind tibia	1.28–1.63	1.45

Associated Termitophiles.—*Thyreoxenus major* Mann (Fig. 1), *Eburniola leucogaster* Mann (Fig. 2), *Termitophya amica* Mann (Fig. 4), *Xenopelta cornuta* Mann (Fig. 5).

Type locality.—Upper Surinam.

Other localities.—British Guiana (Kartabo, Camaria, Kamakusa, Kurupung), Trinidad (Mora forest at 24th mile of Long Stretch Road). All other localities recorded in the literature are from material not distinguished from *N. similis*.

Nasutitermes (N.) similis n. sp.

(Figures 10 and 11.)

Nasutitermes (N.) guayanae (in part) Emerson, 1925, p. 308 (soldier), p. 376 (imago, soldier), Text Fig. 54 (imago, soldier).

Imago: Similar in all respects to *N. guayanae* except that none of the specimens before me approach the very dark brown color of the head, pronotum and abdominal tergites found in some specimens of *N. guayanae* and the ocelli are from one-fourth to one-half their length removed from the eyes in the specimens before me. The winged forms are not fully mature and thus the color of the wings cannot be specifically compared.

MEASUREMENTS IN MILLIMETERS:

	Extremes	Average
Width of head with eyes	1.50 – 1.59	1.55
Long diameter of eye	0.500– 0.543	0.519
Distance of ocellus from eye	0.057– 0.086	0.077
Length of ocelli	0.203– 0.257	0.225
Width of pronotum	1.26 – 1.34	1.29
Length of pronotum	0.71 – 0.80	0.75
Length of hind tibia	1.76 – 1.93	1.82
Length of anterior wing from suture	12.88 –13.16	13.09
Width of anterior wing	3.67 – 3.78	3.72

Soldier (Figs. 7, 10 and 11): Similar in most respects to *N. guayanae* except that none of the specimens before me approach the very dark coloration of some specimens of *N. guayanae* and usually one or two long bristles are to be found near the posterior margin of the pronotum.

MEASUREMENTS IN MILLIMETERS:

	Extremes	Average
Length of head	1.50–1.85	1.67
Width of head	0.92–1.20	1.02
Length of hind tibia	1.15–1.43	1.29

Associated Termitophiles.—*Termitophya punctata* Mann (Fig. 3), *Xenopelta tricornis* (Mann) (Fig. 6).

Type locality.—British Guiana (Kartabo). Type specimens (422) are deposited in the author's collection.

Nasutitermes (N.) columbicus (Holmgren)

Eutermes guayanae, form *columbicus* Holmgren, 1910, p. 256 (soldier).
Nasutitermes guayanae, variety *columbicus* Dietz and Snyder, 1923, p. 282, 298 (biology), Pl. 2 (nest).
Nasutitermes columbicus Snyder and Zetek, 1924, p. 3, 20 (biology), Pl. X (shelter tubes).
Nasutitermes columbicus Snyder, 1924, p. 30 (imago).
Nasutitermes columbicus Snyder, 1925, p. 193 (locality).
Nasutitermes columbicus Emerson, 1925, p. 378 (imago, soldier).
Nasutitermes (N.) columbicus Snyder, 1926, p. 28 (locality).

This species has been reported from Columbia, Panama, Canal Zone and Costa Rica. It has been thought by Dr. T. E. Snyder and by the author that the imago is distinct from *N. guayanae* although the soldiers are quite similar. The further knowledge of variation in *N. guayanae* contained in the preceding pages makes it appear that these species are morphologically identical in both the imago and soldier castes. No character or measurement of imago or soldier (Table II) before me (1 soldier cotype, Columbia; 1 imago, 5 soldiers, Frijoles, Canal Zone; 5 imagoes, Canal Zone) is very distinct from the specimens which I have determined as *N. guayanae* from British Guiana. The color, although similar to specimens of *N. guayanae* not associated with termitophiles, is darker than the reproductive pairs found in nests harboring termitophiles. It is thus possible that a new termitophile series may be found associated with *N. columbicus* and with the dark reproductives from British Guiana. Until such data are collected, however, *N. columbicus* cannot be considered as distinct from *N. guayanae*.

Imago:

MEASUREMENTS IN MILLIMETERS:

	Extremes	Average
Width of head with eyes	1.53 – 1.62	1.58
Long diameter of eye	0.386– 0.430	0.400
Distance of ocellus from eye	0.158– 0.171	0.169
Width of pronotum	1.08 – 1.29	1.18
Length of pronotum	0.71 – 0.74	0.72
Length of hind tibia	1.71 – 1.82	1.77
Length of anterior wing from suture	10.72	10.72
Width of anterior wing	3.43	3.43

Soldier: Pronotum lacking conspicuous bristles near the posterior border in all specimens (six) before me.

MEASUREMENTS IN MILLIMETERS:

	Extremes	Average
Length of head	1.76–1.88	1.82

Type locality.—Columbia.

Other localities.—Panama (Las Sabanas), Canal Zone (Frijoles, Las Cascadas, Barro Colorado Island), Costa Rica (Hamburg Farm).

DISCUSSION

Two species of termites morphologically similar to each other in the same locality raises the question of the mechanisms of speciation in such a case. Field observations failed to indicate that any difference in the ecological adjustment of the two species existed. The nests which are from a foot to two and a half feet high and from a foot to a foot and a half in diameter are attached to trees, either on the trunk or in crotches between branches. They are usually round or oval, composed of wood carton, with a surface covered with small humps and a thin-walled outer portion and a thick-walled inner portion near the royal cell. They occur at various heights above the ground and covered carton runways ascend and descend from the nests and often can be followed some distance along the ground from the nest. The termites are primarily wood eaters and are found in decaying as well as hard wood. Together, they constitute the commonest termites at Kartabo. Following the specific determination, it appears that *N. guayanae* is more abundant than *N. similis*, but I hesitate to make any definite statement to this effect. Further collection records might show them to be equal in colony numbers in a given area. It would appear, therefore, that these species are not only similar morphologically but that they are ecologically equivalent in the same locality.

It would seem to the author that the isolation factor associated with the divergence of these two species is to be found in the close inbreeding commonly observed among termites. Usually brother and sister pairings are observed among swarming termites, in fact there seems to be no authentic record of reproductives from different colonies pairing in nature. Whether pairing from different colonies is rendered difficult by mutual antagonism as suggested by Holmgren (1906) or whether occasionally such cross-breeding may occur cannot be answered with the available data, but certainly close inbreeding is the general rule and by far the commoner type of mating. Thus any chance mutation, series of mutations or chromosome aberrations might become characteristic of a local population which could become sufficiently isolated from the parent population to ultimately result in the origin of a new species with no geographical or ecological barrier. If the germinal changes effected the chemical social mechanisms to a greater extent than the morphological characters, such a condition as is here described could result with a speciation of the associated termitophiles also occurring with the hosts. In this case, speciation of the termitophiles has been accompanied by more morphological divergence than in the case of the host termites. Transfaunation experiments with the termitophiles and the termites should give significant data for a partial solution of some of the problems outlined. Unfortunately such experiments were not tried in British Guiana, the general aspect of the problem not being clear at the time. Cross-breeding experiments would also give valuable information but unfortunately are technically extremely difficult to perform.

Species which are distinguished largely or entirely on the basis of other than morphological characters have been described from numerous groups of animals and are often referred to as 'physiological species' although the distinguishing characters may be only indirectly assumed to have a physiological basis in some instances. Such cases are not common in the literature dealing with multicellular animals because they are difficult to detect and because speciation usually is accompanied by morphological divergence. Subspecies or races with similar morphology and detected by physiological or biological criteria have been described among numerous groups of animals. If the race shows geographical isolation it is termed a 'geographical race' and when it occupies the same territory but shows eco-

logical isolation it is termed a 'biological race.' Thorpe (1930) has given an excellent review and discussion of the various types of biological races found among multicellular organisms. To his bibliography I should like to add the following instances.

Taverner (1926) discusses a case of species distinction among wood pewees (*Myiochanes*) based primarily upon the differences in the call and in geographical distribution. Kinsey (1930, p. 37) discusses cases of morphologically similar species and subspecies of gall wasps (*Cynips*) based largely upon gall characters. Fulton (1931) reports subspecific distinctions of the cricket, *Nemobius fasciatus*, based largely upon ecological distribution, seasonal history and song characteristics, and the same author (1933) carries the study further through breeding experiments. Poulson (1934) reports different times of development for intersterile races of *Drosophila pseudoobscura* which are indistinguishable in appearance, but are geographically and ecologically different. Hackett, Martini and Missiroli (1932) discuss racial distinction in Anophelene mosquitoes on the basis of egg characters, ecological and geographical distribution, and malarial transmission. Lathrop and Nickels (1931) give further data on the morphologically similar biological races of the blueberry maggot, *Rhagoletis pomonella*, with different host plants. Scott (1930) discusses susceptibility to infection in dogs and cats from two physiological strains of the dog hookworm.

The distinction between the categories of race, subspecies and species in these instances is, of course, troublesome and, to a certain extent, arbitrary. It is obvious that speciation is a dynamic process and that these terms apply to various stages in the process which have no well marked and sudden breaks. When the data point to a complete isolation, particularly one of long standing, it seems best to apply the term 'species' to the genetically distinctive populations, whether the distinction is based upon morphological, physiological or psychological criteria, or whether the distinction is qualitative or quantitative. Degrees of divergence may indicate degrees of relationship in cases of speciation involving a multiplicity of slight genetic variations, but in many cases, including the instance here recorded, degree of difference within the species may be much greater than between species.

The example of 'physiological species' reported in the preceding pages is of particular interest because (1) it is the

first instance on record for termites (Isoptera); (2) it is a case of speciation without geographical or ecological isolation, but probably based upon reproductive isolation only; (3) it is one of the few cases on record of physiological speciation in host populations.

SUMMARY

1. Four genera and four species of termitophilous Staphylinidae were found together in certain termite nests and two other species of two of the same genera were found together in other similar termite nests.

2. The genus *Ceratoxenus* Mann is placed in synonomy with *Xenopelta* Mann (Staphylinidae, Aleocharinae).

3. The termitophilous Staphylinidae involved are all monoxenous symphiles. Staphylinid eggs and larvae were found in some nests.

4. Speciation mechanisms among the termitophiles are discussed.

5. Quantitative measurements of the soldier head lengths and the number of bristles near the posterior margin of the soldier pronota are correlated with the termitophile distribution and indicate the existence of two physiologically distinctive termite species formerly determined as *Nasutitermes guayanae* (Holmgren).

6. Dwarf soldiers from young colonies and soldier-worker intercastes show that variations of the castes within the species are much greater than the variations between closely related species.

7. No qualitative or quantitative distinctions were found between the reproductive castes of the two species.

8. Diagnostic characters are given for *Nasutitermes* (*N.*) *guayanae* (Holmgren) and *Nasutitermes* (*N.*) *similis*, n. sp. and their relationship to *Nasutitermes* (*N.*) *columbicus* (Holmgren) is discussed.

9. Speciation mechanisms are discussed which may explain the origin of these morphologically similar, ecologically equivalent, host termites found in the same locality.

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MASS ACTION PHENOMENA IN MEALYBUG WILT[1]

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Pseudococcus brevipes (Ckll.) is a toxiniferous insect capable of producing wilt of pineapples[2]. Although large populations of the insect may develop on a single pineapple plant and in time produce a collapse of the plant which has been designated as "slow wilt," the most severe type of wilt is that known as "quick wilt" which follows when a number of mealybugs are placed simultaneously on a pineapple plant.

Since it has been shown[2] that the toxicity of mealybugs is influenced by the kind and condition of the host plant from which the mealybugs are taken, the "toxic dose" has been standardized at 50 mealybugs removed from the source which proved most toxic in the experiments just referred to. Experiments have shown, however, that on occasion, a much smaller number may produce wilt, typical cases having been obtained with as low as 5 mealybugs.

Two hypotheses are therefore tenable. The first is that all the mealybugs from a single colony are equally toxic and that various quantities of toxic secretion are necessary, dependent on the general toxic level of the colony and the susceptibility of individual plants. The second is that the capacity to produce wilt is limited to individuals in the colony so that wilt ensuing from mealybug attack is governed by the incidence of toxic individuals. The first hypothesis is amenable to a number of experimental approaches. With the second, however, the incidence of toxic individuals may be so low as to require an extremely large experimental population. The present investigation was planned to meet this requirement by providing for the experimental infestation of a sufficiently large number of plants to permit of statistical analysis of the data obtained.

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[2]Carter, Walter. 1933. The pineapple mealy bug, *Pseudococcus brevipes*, and wilt of pineapples. Phytopath., 23 (3): 207–242.

METHOD

Approximately one acre in the Kahuku district of Oahu was made available for the experiment. The field was not in good agronomic condition, was planted without mulch paper, but from the time that the experiment started, received all the usual care.

Plots were arranged in Latin square formation according to Table IV. The entire Latin square was duplicated. Each plot consisted of 80 plants in five 2-row beds of 16 plants each.

Prior to applying the mealybugs the plots were rogued of all plants showing abnormalities, particularly those showing pronounced evidence of previous mealybug attack. Some of these plants were dissected and mealybugs found thereon, indicating that (as is commonly the case), mealybugs were present on the planting material in some degree

TABLE I

WILT OCCURRING IN CHECK PLOTS AND THOSE INFESTED WITH ONE MEALYBUG PER PLANT

Bed Nos.	Check Plot					Infested Plot—One Mealybug per Plant				
	Number of Plants in Plot	1st Wilt Count	2nd Wilt Count	Total	Percent	Number of Plants in Plot	1st Wilt Count	2nd Wilt Count	Total	Percent
1– 5	323	1	0	1	0.31	63	1	0	1	2
6–10	320	1	1	2	0.63	56	1	1	2	4
11–15	296	3	1	4	1.35	66	1	0	1	2
16–20	291	0	0	0	0	69	0	0	0	0
21–25	333	0	1	1	0.30	62	0	0	0	0
26–30	326	1	2	3	0.92	68	0	0	0	0
31–35	286	2	0	2	0.70	64	1	1	2	3
36–40	289	3	0	3	1.04	53	0	0	0	0
41–45	340	3	0	3	0.88	67	0	0	0	0
46–50	347	1	0	1	0.26	68	0	0	0	0
Grand Total	3,151	15	5	20	0.64	636	4	2	6	0.9

when the field was planted. Roguing materially reduced the number of plants available for infestation from 800 to an average of 630. Actual numbers of plants remaining in each plot after roguing are shown in the tables.

Just prior to infestation, the plots were examined again and abnormalities recorded but the plants left untouched.

Infestations of 1, 5, 10, 20 and 40 mealybugs were applied from fields which were entering first ratoon and were selected from plants showing either signs of wilt or growing in close proximity to wilted plants. All bugs used were subgravid and none were forcibly removed from the plants. The method in this case was to dissect the plants and spread the infested pieces out. This disturbed the insects which were removed to Petri dishes only when their mouth-parts had been withdrawn from the plant.

On May 3, two weeks after infestation had been completed, alternate plots were sprayed out. This would theoretically admit of two grades of infestation, one wherein the feeding of the colony was permitted for a limited period only, the other wherein the colony's growth and feeding were unimpeded. The establishment of the colonies, however, in the unsprayed plots followed the usual course where ants fail to appear and, with very rare exceptions, disappeared. Records were taken of the condition of the plants in all plots on May 24, the object being to note abnormalities developing after the plots were rogued, but prior to the expiration of the normal incubation period. Wilt was recorded on July 3 and on August 8.

The data are tabulated in Tables I to IV.

TABLE II

WILT OCCURRING IN PLOTS INFESTED WITH FIVE AND TEN MEALYBUGS PER PLANT

Bed Nos.	Infested Plot—5 Mealybugs per Plant					Infested Plot—10 Mealybugs per Plant				
	Number of Plants in Plot	1st Wilt Count	2nd Wilt Count	Total	Percent	Number of Plants in Plot	1st Wilt Count	2nd Wilt Count	Total	Percent
1- 5	63	2	1	3	5	71	6	2	8	11
6-10	49	2	0	2	4	59	2	2	4	7
11-15	60	3	2	5	8	60	2	3	5	8
16-20	58	4	0	4	7	59	2	2	4	7
21-25	57	3	1	4	7	65	2	2	4	6
26-30	64	5	2	7	11	62	6	3	9	15
31-36	55	3	1	4	7	57	5	2	7	12
37-40	56	5	1	6	11	55	14	1	15	27
41-45	66	4	3	7	11	74	8	4	12	16
46-50	71	3	2	5	7	71	4	0	4	6
Grand Total	599	34	13	47	7.8	633	51	21	72	11.9

STATISTICAL ASPECTS OF THE PROBLEM

If we assume that we have, in every population of mealybugs, some individuals which are toxic and others which are non-toxic, we can calculate the numbers of plants which would be expected to wilt since the distribution of toxic individuals would follow the laws of chance and accordingly the incidence of wilted plants would also be a matter of chance. If there are approximately equal numbers of toxic and non-toxic bugs the expected numbers of wilted plants could be determined by the expansion of the binomial $(p + q)^n$. If the incidence of toxic individuals is small, the number of plants which would have no toxic bugs would be determined by the Poisson exponential expansion[3].

[3]Soper, H. E., Biometrika, 10: 25, or K. Pearson, Handbook for Biometricians and Statisticians, Part 1, pp. lxxvi-lxxvii and pp. 113-121.

If we assume that every bug carries a small amount of toxic material not in itself of sufficient quantity to cause wilt symptoms, it would be expected that the incidence of wilted plants would follow the law of mass action or be proportional to the numbers of bugs applied per plant. If wilt occurred in simple proportion to the number of mealybugs applied it should then be a simple matter to produce 100 percent wilt by increasing the number of mealybugs. Experience has shown this to be an extremely difficult thing to achieve. A theoretical curve has not been calculated for the expected results following the law of mass action since such curves tend to follow trends similar to Poisson series.

TABLE III

WILT OCCURRING IN PLOTS INFESTED WITH TWENTY AND WITH FORTY MEALYBUGS PER PLANT

Bed Nos.	Infested Plot—20 Mealybugs per Plant					Infested Plot—40 Mealybugs per Plant				
	Number of Plants in Plot	1st Wilt Count	2nd Wilt Count	Total	Percent	Number of Plants in Plot	1st Wilt Count	2nd Wilt Count	Total	Percent
1– 5	64	13	5	18	28	63	19	5	24	38
6–10	55	12	0	12	22	67	10	3	13	19
11–15	67	15	3	18	27	56	14	4	18	32
16–20	60	8	2	10	17	62	11	11	22	35
21–25	67	9	2	11	16	62	15	5	20	32
26–30	64	8	3	11	17	67	18	1	19	28
31–35	54	7	0	7	13	57	16	8	24	42
36–40	58	16	3	19	33	60	27	2	29	48
41–45	63	13	4	17	27	69	32	3	35	51
46–50	74	6	1	7	9	73	20	3	23	32
Grand Total	626	107	23	130	20.8	636	182	45	227	35.7

The two hypotheses are compared for three different hypothetical toxicity values in Figure 1. It is seen that when the incidence of individual toxic bugs is 0.1 percent the resulting expectancy of wilt is coincident with a proportion in which 100 bugs would be expected to cause 10 percent wilt. When the incidence of toxic bugs becomes 1 percent there is a deviation from the expected results on a basis of a simple proportion 100 to 100. The last set of curves compares the incidence of toxic bugs of 20 percent with a proportion of 10 to 100. We know, however, from the experience of other mass-action curves that they do not follow simple proportion but tend to follow trends similar to the Poisson series. The significant thing to be gathered from these comparisons is that we may never hope to separate mass action and individual toxicity statistically from this line of reasoning unless it is possible to determine that there is a threshold of toxicity of such magnitude that it can be shown statistically that more than one mealybug must be present to cause wilting of an individual plant.

We might apply the Chi-square test of goodness of fit of our empirical results and show that good agreement had been shown to exist between observation and either of these hypothetical curves and yet we might

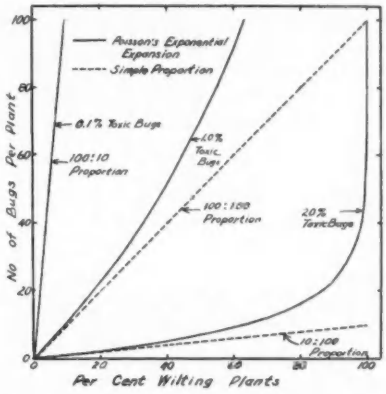

FIG. 1. Theoretical curves indicating the expected collapse of pineapple plants when varying numbers of bugs are applied.

draw erroneous conclusions from the analysis. If a threshold of toxicity can be demonstrated, where more than one bug is required to cause any plant to wilt the results undoubtedly are due to a mass

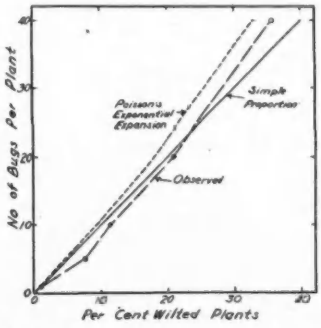

FIG. 2. Results of actual experiment applying varying numbers of mealybugs to pineapple plants compared with that to be expected following simple proportion and with the Poisson exponential expansion.

action phenomenon but if by coincidence the threshold of toxicity is so low that individual bugs may have the threshold toxic dose we will never be able to separate individual toxicity phenomena from those of mass action.

STATISTICAL ANALYSIS OF THE DATA

The results of actual experiment are summarized in Table V and graphed in Figure 2, and are compared with the expected values calculated on the basis of the Poisson series and on simple proportion. Considering the high probable errors and the variability, a good fit could be shown to either hypothesis. This is to be expected since the expectancies in either case are not markedly dissimilar. The data, however, do show that there is no significant difference between the checks and the series where a single bug was put on a plant. In the

TABLE IV

ARRANGEMENT OF PLOTS AND PERCENTAGE OF PLANTS WILTED IN EACH PLOT AT THE END OF THE EXPERIMENT. CHECK PLOTS AND C PLOTS OMITTED. NUMBER OF MEALYBUGS APPLIED PER PLANT: A–10; B–20; C–1; D–40; E–5

A 11	D 19	B 27	C	E 7	A 15	D 42	B 33	C	E 7
E 5	B 22	C	D 35	A 6	E 11	B 13	C	D 51	A 6
D 38	A 7	E 8	B 17	C	D 28	A 12	E 11	B 27	C
B 28	C	A 8	E 7	D 32	B 17	C	A 27	E 11	D 32
C	E 4	D 32	A 7	B 16	C	E 7	D 48	A 16	B 9

series where 5 bugs were put on a plant there is considerable significance of the difference between this concentration of mealybugs and the checks. This indicates that a true threshold of toxicity exists between 2 and 5 bugs per plant. For the present argument we are not concerned with the exact level of this threshold save that it be greater than one bug per plant. Since this is the case we are justified in concluding that the results are due to a mass action phenomenon where each bug carries an amount of toxic material not in itself sufficient in amount

to cause any plant to wilt and not to a random distribution of bugs some of which are toxic and others of which are non-toxic.

DISCUSSION

It is evident from the data presented that there are inherent difficulties in separating mass action phenomena from those of toxic incidence, by statistical methods. When the factor of plant susceptibility is considered these difficulties are greatly increased since there is no numerical expression available for plant susceptibility.

It may be assumed, however, that variability in this last respect was offset by the Latin square arrangement of plants and the large number of plants used, so that the significant difference between wilt counts in check plots[4] and those infested with 5 bugs can be considered

TABLE V

ACTUALLY OCCURRING WILT FOLLOWING INFESTATION BY VARYING NUMBERS OF MEALYBUGS COMPARED WITH EXPECTANCIES AS SHOWN BY SIMPLE PROPORTION AND POISSON'S EXPONENTIAL EXPANSION

Number of Bugs per Plant	Observed Wilt, Percent	Expected	
		Simple Proportion, Percent	Poisson's Exponential Expansion, Percent
40	35.89 ± 1.90	40	33.0
20	20.93 ± 1.53	20	18.1
10	11.51 ± 1.35	10	9.5
5	7.77 ± 0.49	5	5.0
1	0.98 ± 0.28	1	1.0
Check	0.64 ± 0.09	0	0

an adequate datum on the existence of a "threshold toxicity" in that case which was greater than unity.

Certain other observations mitigate against the hypothesis that wilt is the result of incidence of toxic individuals. *Pseudococcus brevipes* is a parthenogenetic insect and, when once established on a plant which provides suitable food, is practically sedentary.

It is difficult to conceive of very great variation in toxicity among individuals of a colony which may have arisen from one or two mothers and which have spent their entire lives on the same narrowly restricted area of feeding which a pineapple plant provides.

[4]Although all the plots were severely rogued prior to the application of the experimental infestations it should be recalled that the incubation period of mealybug wilt is rarely less than two months. The occasional wilt occurring in the checks and plots infested with one mealybug after roguing is not surprising in view of the impossibility of detecting all the abnormal plants at the time the plots were rogued.

The development of control measures against *Pseudococcus brevipes* has also shown that the presence of individuals or very small colonies of the insect may be quite general but no wilt ensues until these colonies have built up and dispersed in large numbers to surrounding plants.

SUMMARY

In an experiment on the relationship between numbers of mealybugs applied and resulting wilt of pineapple plants, 3,130 plants were infested with mealybugs varying in number from 1 to 40, and 3,151 check plants were observed.

It has been shown that the separation of mass action phenomena from those of incidence of toxic individuals by statistical methods is difficult but wilt in the plots infested with one mealybug per plant was not statistically significant when compared with that developing in the check plots. From this it is concluded that under the conditions of plant susceptibility prevailing at the time, the most susceptible plant required a toxic dose greater than that provided by the feeding of one mealybug.

The biology of the insect and field observations on its occurrence provide additional evidence against the hypothesis that wilt is the result of the incidence of toxic individuals. The datum on the factor of mass action is indicative but other experimental approaches will be necessary before this factor can be adequately evaluated.

AN EDITORIAL APOLOGY AND CORRECTION

On page 240, Volume XXVIII, of the Annals of this Society the Managing Editor made a statement as follows: "One new species after another was scooped * * *. The last scoop was accomplished by one who had had the privilege of studying the manuscript and who rushed two papers through by publishing privately after the present volume was on the press." We retract the above and apologize to the author to whom it appears to apply. Though we did not remember the writer's name at the time the above statement was written, we were under the impression that the statement was a sound conclusion from the fragmentary information we used from three different sources.

We wish to thank our friend who, by letter, has called our attention to this grevious error. Our friend is familiar with all the circumstances, and states concerning the privately published papers: "His privately published work does not have a single species that antedates one in the Betten book. The only 'manuscript' seen by that writer was a few pages of galley proof sent to him by Doctor Betten." On this letter we base the above correction and apology.

CLARENCE H. KENNEDY, *Managing Editor.*

BIOLOGICAL NOTES ON URANOTAENIA SPP. IN LOUISIANA (CULICIDAE, DIPTERA)

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This interesting group of tiny mosquitoes has three representatives occurring in the United States, two of which have been found in Louisiana. *Uranotaenia anhydor* is apparently restricted to California. The general appearance and position of the larvae in the water, when at rest, is strikingly similar to that of *Anopheles* and casual examination might pass them over for this genus since they are almost horizontal and just beneath the surface film. They seem to feed and spend the majority of their time at the surface but when disturbed, rapidly seek the bottom and may remain there for considerable time.

Their life cycle has been partially known for years, the eggs being laid in small rafts on the surface of the water but little information exists as to the length of the larval instars, etc. The biting and hibernating habits of the adults are matters of dispute. From an economic point of view, this genus assumes little importance but their habits make them of some interest. It is hoped that the following notes will add some information as to the life history of *Uranotaenia sapphirina* and *lowii*.

Uranotaenia sapphirina Osten-Sacken

According to Dyar (1928) this species is distributed throughout the Eastern United States from New Hampshire and New York to Florida and Texas, Honduras, Antilles and Virgin Islands. The larvae live in ground pools of a semi-permanent nature such as commonly harbour *Anopheles* larvae. This author states that the adults will bite under favorable conditions but are seldom met with. Dyar (1922) is of the opinion that the winter is passed in the adult stage. Felt (1904) found the larvae of this species in early August in New York and believes that the species breeds throughout the summer. Headlee (1921) records larvae from New Jersey in June, August and September and doubts that the females suck blood. Theobald (1907) states that "the larvae are fond of resting below the leaves of *Lemna*. This species breeds all summer, preferring warm stagnant pools containing *Spirogyra*. It is a local breeder being found in and about the same places each year and always in permanent bodies of water. It is not known how the winter is passed." Beyer (1923) gives records

of this species from Louisiana in March and June. Viosca (1924) reports the capture of single females of this species during June, September and October. Bishopp, Cory and Stone (1933) found them in the Chesapeake Bay section during the late summer and fall, with the greatest abundance early in summer.

The writer first found larvae of *Uranotaenia sapphirina* in a large, permanent pool filled with water hyacinth (*Piaropus crassipes*) near Raceland, La., June 28, 1931 associated with *Anopheles crucians* and *Corethrella brakeleyi* larvae. While studying the hibernation of *Anopheles quadrimaculatus* in Fort Jackson (Hinman, 1934) enormous numbers of female *Uranotaenia sapphirina* were observed within the Fort during the latter part of December. They were especially abundant about the dark moist crevices in the walls and in a single sweep of about two feet, over a thousand females were captured in a net. More than half of these were *Uranotaenia sapphirina*. These insects were not evenly distributed throughout the Fort but many millions must have been present. The end of December, 1934, these insects were again so abundant around certain damp corners of the Fort that several might be collected in the space of one square inch. Certain individual bricks provided a resting place for over a hundred. Actually millions of them were present. In spite of this abundance, not a single larva could be found in twenty minutes of dipping in the moat surrounding the Fort. During January and the early part of February, these insects were abundant, but by February 20th, there was a marked diminution in numbers and on March 27th no adults could be found. While every attempt possible was made to get the females to suck blood, the writer has never observed a single one biting. During December and January and early in February, the females were very easily disturbed, suggestive of false hibernation; however, none of these were ever observed actively flying about outside the Fort.

In spite of the enormous numbers of females found resting in the Fort during the winter, larvae have never been recovered except in very small numbers from the moat surrounding the Fort or from other breeding pools in the immediate vicinity. Because of the few larvae captured, it is impossible to determine how many broods there are per year. Larvae have been found as early as the middle of March and an egg mass was secured as late as September 18th. It is believed that this species may pass the winter either in the larval stage or as hibernating females. It seems most remarkable that such a rare mosquito is able to congregate in enormous numbers to pass the cooler months.

Larvae were captured early in January near New Orleans in connection with the C. W. A. pest mosquito control project. The writer also collected larvae of this species in a pond at Dexter, Michigan on August 13, 1934, which extends the records of this mosquito.

Uranotaenia lowii Theobald

Dyar (1928) gives the distribution of this species as Gulf States, Antilles, Panama, Ecuador, Columbia, Venezuela, Trinidad, the Guianas and Argentina. He states that the larvae occur in ground pools, principally the grassy margins of lakes and that the adults are

not known certainly to bite. Theobald (1903) reports that imagines only lived but two days, seemed very delicate and reufsed to bite. He quotes Hewlett as finding them rare in Trinidad, occurring in August and biting severely. According to Beyer (1923) adults have been reported from Baton Rouge and New Orleans, Louisiana. Dyar and Shannon (1924) found the species in Florida as late as December.

The writer first found larvae of this species in Audubon Park, New Orleans, in a pool densely filled with *Myriophyllum verticillatum*. This pool has been under observation for the past two years and only once has it dried up, when the water course was slightly changed. (March, 1934, it was entirely cleaned out as part of C. W. A. project). It is supplied by the city water system. During 1932 larvae and pupae were present throughout June and July. In 1933 larvae and pupae were found as early as May and as late as September. A few larvae were also found at Fort Jackson in September. Throughout this period it has been customary to find larvae of all stages present at the same time. In the laboratory, development proceeds at a normal rate with the pupal period averaging twenty-four to forty-eight hours. However, it is possible that development is somewhat delayed in the feld and that this long breeding season represents very few broods. Egg masses have never been encountered. Adults have never been captured in the wild except amongst the emergent vegetation of the breeding pool or upon the surface of the water. Reared females exhibit a marked tendency to rest upon the surface of the water. Under no conditions have they been induced to suck blood. No information has been secured as to the manner in which this species passes the winter. Never have they been found within Fort Jackson.

TAXONOMICAL STUDIES

While the adults of *Uranotaenia sapphirina* and *lowii* are very distinct and can be readily distinguished in the field both by their markings and by the smaller size of *U. lowii*, yet the larvae are remarkably similar. From a detailed study of both cast skins and mounts of whole larvae (75) the writer has come to the conclusion that it would be unwise to try to separate the larvae of the two species upon the minute and inconstant differences which he has found. It is true that there is a slight difference in shape of the antenna, in position of the antennal hair and length of pecten, etc., as noted by a tabulation of a large number of characters for each of the larvae examined but no single constant character was observed. The United States National Museum kindly loaned its specimens of larvae of these species and Dr. Robert Matheson supplied *U. sapphirina* from New York State.

DISCUSSION

In Louisiana *Uranotaenia* spp. have been found to be very local and selective in their breeding habitats. Larvae of both have been taken in permanent or semi-permanent pools only. While *Uranotaenia sapphirina* hibernates as adults nothing is

known as to the manner in which *U. lowii* passes the winter. Neither of these species has ever been induced to suck blood. The length of the life cycle under natural conditions has not been accurately determined but laboratory rearing indicates a period of not more than three weeks during the warm season. Breeding in both species seems to be continuous throughout the spring, summer and fall seasons and in the case of *U. sapphirina* may extend throughout the winter.

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INSECTS OF PUERTO RICO AND THE VIRGIN ISLANDS. HOMOPTERA (EXCLUSIVE OF STERNORHYNCHI), by HERBERT OSBORN. pp. 111–260, figs. 1–71. 1935. Published as Part 2, Volume XIV, of the Scientific Survey of Porto Rico and the Virgin Islands by the New York Academy of Sciences. Price, $2.00, from N. Y. Acad. Sci., 77th St. and Central Park West, New York.

This very comprehensive survey of Puerto Rico and the Virgin Islands is now in its sixteenth volume. It covers the fields of geology, botany and zoology. The publication of the reports is financed through the New York Academy of Sciences. To date the only groups of insects that have been monographed are a part of the Lepidoptera Heterocera, by W. T. M. Forbes; the Diptera, by C. H. Curran; the Odonata, by Elsie B. Klots, and the Homoptera, by Herbert Osborn.

The volume on Homoptera opens with an interesting discussion of the relationships of the Puerto-Rican fauna. Apparently the fauna has affinities to the areas west (Central America and Mexico) rather than to South America. This agrees with the conclusions of botanists and others. The fauna is not rich in species, 150 species being listed. This is partly due to long continued geological isolation and partly to man's despoilation of the native flora. The seventy illustrations are mainly the product of the artist, Mrs. C. W. Taft, and are beautifully drawn.

C. H. K.

BOOK NOTICES

PRINCIPLES OF INSECT MORPHOLOGY, by R. E. SNODGRASS. Pages i-ix and 1–667, 319 figures, 1935. Published by McGraw-Hill Book Company, Inc., New York and London. Price, $6.00.

The subject matter of this treatise is divided into twenty-one chapters as follows: Chapter I, Introduction; II, Organization and Development; III, Body Wall and its Derivatives; IV, Body Regions and Segmentation; V, Segmental Appendages of Arthropods; VI, The Head; VII, Head Appendages; VIII, Thorax; IX, Thoracic Legs; X, Wings; XI, Abdomen; XII, Organs of Ingestion; XIII, Alimentary Canal; XIV, Organs of Distribution, Conservation and Elimination; XV, Respiratory System; XVI, Nervous System; XVII, Sense Organs; XVIII, Internal Organs of Reproduction; XIX, Organs of Copulation and Oviposition. References occupy pages 625 to 646 and the Index pages 647 to 667. Except a few redrawn by the author from other sources, the three hundred or more illustrations are by the author himself. Each chapter is divided into sections by the regular use of three types of subheads and each ends with a glossary of terms applied in that chapter. This is the most conveniently arranged glossary we have seen.

We quote from the author's Preface. "Each of the several chapters of this book * * * is an attempt to give a coherent morphological view of the fundamental nature and the apparent evolution of a particular group of organs or associated structures. It is more than likely, practically certain, that many of the generalizations here offered will soon be modified or superseded by other generalizations, but they will have served their purpose if they induce critical students to make a wider and more thorough study of the problems of insect morphology."

Snodgrass is a student who has never been given to making generalizations on slender evidence. He is first of all an observer with a remarkable ability in describing lucidly what he has seen. This lucid use of simple language is then further cleared by unusual ability in simple illustration. Those who have observed his research state that in any controversial problem he always dissects more insects, until he is satisfied as to the facts. Except for a short excursion into commercial illustration Snodgrass has been dissecting and drawing the parts of insects since 1899. Thus this volume is the result of an extended and mature experience.

Much of the matter presented has appeared in the various papers by the author, particularly the series in the Miscellaneous Collections of the Smithsonian Institution. In this volume that material with additions has been brought together, reorganized and balanced. It is the balance of material which characterizes the present presentation of the subject. No phase is expanded at the expense of other equally important subjects.

The reviewer hopes that the terminology in this work can be generally used so that the book can be considered a reference work in this phase of the subject. Snodgrass has no axe to grind in the matter, because he has never advocated any particular system. He has been conservative in the use of terms. He states: "In preparing the present text the writer has made a special effort to concur with the authors of these books (Imms and Weber) in the matter of anatomical terms, in order that students may be spared confusion in turning from one treatise to another. Unfortunately however, there is still much unavoidable discrepancy in the use and application of anatomical names in entomology. The trouble, in large measure, can be blamed on the insects themselves, since they will not entirely conform with any plan of nomenclature or with any scheme we can devise for naming their parts consistently."

Words of praise are no longer needed in discussing the writings of Snodgrass. They have all been applied in the years past to his earlier works. No recommendation of the "Principles of Insect Morphology" is needed as entomologists have been looking forward to the appearance of this work. It is necessary in the library of every working entomologist since no insect escapes being burdened with body structure.

The work has the usual format of a McGraw-Hill text in its excellent paper, printing and sound binding.—C. H. K.

LIMNOLOGY, by PAUL S. WELCH, pp. i–xiv and 1–471, 53 tables and 46 figs. 1935. flublished by McGraw-Hill Book Company, Inc., New York and London. Price, $5.00.

During the past forty years many noteworthy contributions to the study of Limnology have originated in America. The bulk of the material has come from a few investigators. With the recent recognition by politicians of the problems of conservation of natural resources we suddenly realized that America had very few investigators completely trained in limnological research. Limnology, in its heavier aspects, has always been a cold, wet, messy business which has attracted few students. The earlier investigators made little effort to train successors. Professor Welch, after joining the staff of the Douglas Lake Station of the University of Michigan, recognized this lack and deliberately set to work to acquire a knowledge of limnological methods and to organize this in form for zoological students. A year was spent studying methods in European stations after which the work at the Douglas Lake laboratory was taken up, and courses were introduced at the University.

This volume airs no theories. It is a sound and well organized compilation of the best in our present knowledge of the subject. With his command of precise English, Professor Welch has given us a very clear and readable outline of the subject.

The subject matter is treated in five parts: Part I, Preliminary Considerations; Chapter I, Introduction; II, Fresh-Water Environments; III, Lakes, Their Origin and Diversity. Part II, Nature of Fresh-Water Environments; Chapter IV, Physical Conditions; V, Chemical Conditions. Part III, Biological Relations; Chapter VI, Influence of Physical Conditions; VII, Influence of Chemical Conditions; VIII, Organisms in Inland Waters; IX, Plankton; X, Bacteria, Other Fungi, etc.; XI, Higher Aquatic Plants; XII, Necton; XIII, Benthos; XIV, Biological Productivity. Part IV, Special Types of Lentic Environments; Chapter XV, Ponds; XVI, Bog Lakes. Part V, Lotic Environments; Chapter XVII, Running Waters in General. Bibliography. Index.

This is a volume fit to take its place beside some of the recent summaries of plant ecology which is an older and simpler field of research. Limnology is on a narrow field of more uniform conditions so that it does not show the great gaps of knowledge found in the majority of general animal ecologies that try to deal with both land and water animals.

The volume is of interest to entomologists as it deals with the various very specialized insects that have succeeded in penetrating the aquatic environment. Insects were evolved as land animals, then by various curious adaptations a few groups have succeeded in invading an environment for which their basic structure was not originally adapted. Because they are perverted curiosities of aquatic life they have received more than their share of attention in the earlier literature of limnology. Because of the obviousness of the added adaptations of insects which permit their entrance into the water environment they call attention to the conditions to be met more vividly than do many of the animals more fundamentally organized for the aquatic life.

This volume is the first comprehensive and sound review of limnology in the English language. It gives a firm starting point for students of the subject. It is well bound and is printed on excellent paper, a credit to the publisher and the author.—C. H. K.

FORMICIDAE UKRAINAE, by W. KARAWAJEW, pp. 1–162 and index, two pages; 39 text figures. Published as a volume (unnumbered) in the Series, "Travaux systématique et faunistique" of the Ukrainian Academy of Sciences, 1934. Kiev, Ukrainia.

Professor Karawajew, a world authority on ants, has given us in this volume what is apparently the first part of a work on the ants of his home region. Thirty-nine species of Palaearctic ants are treated. Two of these are Ponerine ants, the remainder Myrmicine. It is interesting to an American student of ants to see how closely the series of genera follow the series of genera found across the northern United States and southern Canada. Eleven of the sixteen genera and seven of the species occur in the northern states. It is the same general Holarctic fauna except for a few genera, and some species and varieties.

The first forty-eight pages are devoted to the structure and habits of ants. This carries its own index (pp. 40, 41) in Russian and in Latin. Its illustrations, fourteen in number, are largely from other writers. Figure 11 of the genitalia of the male Formica, credited to Emery, fails to show the subgenital plate in its whole extent. This is characteristic of ant literature in general and not a specific criticism of the author's work.

The reviewer is particularly interested in trying to find specific and varietal characters of ants that can be depicted in illustration. He is almost wholly eye-minded. Taxonomic work in American ants will not be in good shape until such characters of form as exist are found and figured. Just yesterday the males of several forms of Formica were examined and the subgenital plate appeared to have distinguishable specific and even varietal characters, characters of curve and proportions not describable in words, but obvious in figures. The parts of the genitalia themselves carried characters but apparently of less value.

The original descriptions of ants are largely on the degenerate female workers as these are the ants of the field for eleven months of each year. Even some experienced ant specialists do not know species of male ants at sight. Yet the final characters for a sound taxonomy are probably in male structures. As in other social Hymenoptera worker ants have a way of varying within a species from region to region and even from one local habitat to another. Some have nest workers different from field workers, fall and winter forms more different from each other than are well defined species from each other. It is baffling when dependence is placed on written descriptions of worker forms.

Wheeler and Wheeler-students have begun to clear much of this ground, but ant taxonomy appears to be in the condition that occurred in the taxonomy of the Odonata before 1890 when Calvert began work and later Williamson and Walker. It was cleared up by the most arduous of work and by exact illustration.

In spite of implied criticism, Karawajew's work is well illustrated as figures are included for each species. However, he is not dealing with the closely related forms found in the North American fauna.

For a recent Soviet publication it is well printed and on fair paper. The general text is in Russian, the specific descriptions in German. From the title page we quote the following: "Prolétaires de tous les pays, unissez vous!"

—C. H. K.

ENTOMA, A Directory of Insect Pest Control, Listing Insecticide Manufacturers, Insecticides, Chemicals used in Insecticides, Insecticide Machinery, Entomological Supplies and Equipment, Biological Testing Laboratories, Consulting Entomologists or Chemists, Insect Pest Control Companies, etc. Edited by C. C. HAMILTON, pp. 1–101, (pp. 1–35, advertising). 1935. Published by the Eastern Branch of the American Association of Economic Entomologists. Distributed by C. C. Hamilton for the Association, Dept. of Ent., Rutgers Univ., New Brunswick, N. J. Price, 50 cents to all non-members.

This trade publication will be found of use to professional economic entomologists. Its table of contents runs as follows: Advertisements, Insecticides and Materials, Entomological Supplies, Insecticide Machinery, Pest Exterminating Companies, Companies caring for Trees, Publishers of Entomological Books, Biological Testing Laboratories, Parasites (for sale), consulting Entomologists, Information on Insecticides, Index to Advertisements.

We quote from the Foreword: "This directory has been prepared to assist entomologists and others in obtaining certain kinds of information which have heretofore been somewhat difficult of access. The advertisements have been prepared to furnish information which could not be given in the section on listings."

Pages 35–82 contain the "Directory" of persons and companies selling services or products. Pages 82–101 contain a very condensed summary of the principles of insect pest control.

The project was financed from the sale of advertising space and the sale of copies to non-members of the Association. It is a creditable piece of work on the economic rather than scientific side of Economic Entomology and will be of great use to the men who apply the findings of the science.—C. H. K.